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Founded December 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

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Growth stages of Florida Scrub Jays. Top left: a pipped egg and two young, age day 0. Top right: three young, age day 5, in cooling stance with necks stretched over nest rim. Bottom left: usual banding age, day 11, when primaries are breaking from their sheaths. Bottom right: a recent fledgling, age day 18.
GROWTH AND SURVIVAL OF YOUNG
FLORIDA SCRUB JAYS

Glen E. Woolfenden

Few studies of growth in passerines pertain to jays (Corvidae: Garrulinae), and fewer still to group breeders. As a possible contribution to both topics, I measured growth rates of young Florida Scrub Jays (Aphelocoma c. coerulescens) raised by breeding groups of varying sizes. A notable exception to the paucity of information on corvid growth is the recent work on Piñon Jays (Gymnorhinus cyanocephalus), a highly social, colonial breeder that nests early in a north temperate climate (Bateman and Balda 1973). Certain comparisons are made with this species.

Florida Scrub Jays almost invariably remain in their natal territory for more than a year; therefore it was possible to obtain numerous post-fledging measurements and to monitor survival of known-age jays. The growth measure used in the analyses of survival is weight.

Florida Scrub Jays breed either as unassisted monogamous pairs or in groups consisting of a pair and several helpers. Brood size varies from 1 to 5; usually it is 3 or 4, and the number of feeders has varied from 2 to 8. Pairs with helpers fledge more young than do the unassisted pairs (Woolfenden 1975).

preceding the weight data are brief descriptions of general development and the linear growth of certain extremities (see also frontispiece). This information should be useful for aging nestlings whose hatching dates are unknown.

MATERIALS AND METHODS

The data on growth and survival were obtained at the Archbold Biological Station in Highlands County, Florida, where a marked population of Florida Scrub Jays has been under observation since 1969. Individual jays were measured daily or, in a few cases, every other day throughout the nestling stage in 1973 when 47 nests were found, which represented virtually all nesting attempts by 28 pairs, 25 of which produced young. The approximately 136 eggs laid yielded 73 nestlings and 41 fledglings (1.5 per pair), almost
all of which were measured in the course of this study. The productivity data show that 1973 was a near-average breeding year (Woelfenden 1973). Some measurements of nestlings and fledglings also were taken in 1974 and 1975; however, except where otherwise stated, my various analyses of growth incorporate only the 1973 measurements.

Most of the marked birds lived in open habitat, namely sparse oak scrub (Woelfenden 1969 census no. 52, 1973), and some parent and helper jays scolded loudly at human intruders. Thus nest visits by investigators were brief, lasting only a few minutes, in an attempt not to alter normal nest predation. When measuring, we removed all young from the nest simultaneously and moved several meters away; this reduced the intensity of scolding by the older jays. In addition, most nest visits were made in early afternoon (12:30-15:30) when diurnal predators seemed less active, and so that several hours of sunlight remained for the odors we left to dissipate before nocturnal predators became active. These procedures precluded obtaining detailed notes on morphological and behavioral ontogeny.

Day 0 designates the day of hatching. Fledgling and yearling are defined as before (Woelfenden 1973): fledgling is applied to a jay from the instant it leaves the nest until it is 1 year old. A yearling is a jay in its second year of existence.

The ratio between the number of jays supplying food and the number of nestlings being fed is termed the feeder index. It has ranged from 0.4 to 3.0. Nestlings with a 0.4 feeder index were members of a brood of 5 fed by a pair with no helpers; the 3.0 feeder index represents a lone nestling fed by a pair with 1 helper.

Five measurements were taken to the nearest 0.5 mm on each young jay: length of beak, tarsus, primary 7, and longest central rectrix (hereinafter referred to as a deck), and weight. The beak was measured from the anterior end of the nostril to the tip, the tarsus in a standard fashion as the diagonal from the joint with the tibiotarsus behind to the joint with the middle toe in front. The primary and the longest deck were measured from the place of attachment with the skin to the tip of the papilla or feather. Falconers use the term deck for a central rectrix and it is used here not only for brevity but also to emphasize a function of the central rectrices of shielding the lateral rectrices from abrasive wear. In Florida Scrub Jays the decks often become extremely ragged prior to replacement. Weights were taken with Pesola spring balances which were checked regularly for accuracy.

The expressions significant and highly significant are used only in the statistical sense to signify probability at the 5% and 1% levels, respectively.

Asynchronous hatching confounds the problem of measuring growth during brief once-a-day visits to nests, and in the Florida Scrub Jay hatching of eggs from the same clutch sometimes spans more than 1 day. In 1973 eggs from 9 of 25 nests probably had a time span for hatching of between 1 and 2 days. For 4 of these 9 nests, a time span between 1 and 2 days was known, and for 1 additional nest a span of 2-4 days occurred between the hatching of the first egg and last egg. The nestlings were not marked until over 1 week old, and 1 assumed the smaller young in such nests were the younger. In certain instances individual peculiarities allowed identification of these individuals.

Variation in time of fledging is another problem that vexes those who study growth of young birds. If undisturbed, young Florida Scrub Jays remain in the nest several days past earliest possible fledging age. In 1973, when nestlings were handled daily or every other day, almost all fledged when 15 or 16 days old, and only 1 healthy nestling remained through day 17. In 1975, when young jays were handled only on day 11, and thereafter nests were checked from convenient distances, most young fledged when 17 or 18 days old, and a few remained through days 19 to 21. Enticing their young from the nest does not seem to be an important part of Florida Scrub Jay behavior, and perhaps many nests
are vacated between days 14 and 19 because of exogenous disturbances. Earliest fledging has occurred between days 12 and 14 (1 brood), the latest on day 20 or 21 (2 broods). These generalizations are based on observations at approximately 120 successful nests.

GENERAL DEVELOPMENT

At hatching Scrub Jays are naked, as typifies jaybirds, and the skin is reddish-pink, nearly identical in color to the skin of a person's hand when flushed with blood. The viscera, especially the liver, show clearly through the thin and weakly pigmented skin. The beak and legs are pale yellow. Through day 1 they get darker pink, then during days 3–4 yellowish pink. On day 2 they match the color of one's palm when it is drained of blood, and on day 3 they have the color of jaundiced human skin. During day 3 the skin becomes purple-black, usually on the back first, and the young match in color heavily bruised human skin. Darkening progresses through days 4–6 until the young are dark gray-black over most of the body, and especially dorsally. The beak becomes shiny black, the podothecae dull black.

Parting of the eyelids in nestling Scrub Jays is gradual and variable. For a few individuals the process begins as early as day 2, for some the eyes are still closed on day 9. For the majority the eyes open during days 4 through 7. Often in the same individual one eye begins opening before the other.

GROWTH

Tables 1 and 2 and Fig. 1 summarize data on growth of nestlings: they are based only on young hatched in 1973. Table 3 presents information on fledglings, for which birds hatched both in 1973 and 1974 were used. In order to provide a smooth transition in the growth data from nestlings to fledglings, the 0.5-month-old young in Table 3 are the same 20 15-day-old young in Tables 1 and 2.

Feathers.—Papillae of several tracts on the dorsum protrude prominently from the skin about day 4. Primary 7 is at least 1 mm long by day 7; the longest deck is at least 2 mm long by day 13 (Table 1). Feathers of the femoral and posterior dorsal tracts and secondary coverts of the alar tract usually break from their sheaths about day 9, with the earliest on record day 7. Primary 7 erupts between days 10 and 13, usually on day 11, and the decks erupt between days 11 and 15, usually on day 14. This rate and pattern of feathering means that young Florida Scrub Jays are only sparsely feathered until but a few days before they fledge.

The longer 7th primaries of adult-plumaged jays (age in months 24+) versus 6–12-month-old birds (Table 3) are new feathers, the original primaries having been replaced during the complete second prebasic molt. The juvenal
Table 1

Primary 7 and Deck Lengths (mm) of Nestling Florida Scrub Jays

<table>
<thead>
<tr>
<th>Age in days</th>
<th>Seventh primary</th>
<th></th>
<th>Longest deck</th>
<th></th>
</tr>
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<td>N</td>
<td>x</td>
<td>S.D.</td>
<td>Range</td>
</tr>
<tr>
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<td>49</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
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<tr>
<td>2</td>
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<td>-</td>
<td>-</td>
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<td>3</td>
<td>59</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>4</td>
<td>57</td>
<td>0.01</td>
<td>0.07</td>
<td>0-0.5</td>
</tr>
<tr>
<td>5</td>
<td>33</td>
<td>0.45</td>
<td>0.52</td>
<td>0-1.5</td>
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<td>6</td>
<td>34</td>
<td>1.49</td>
<td>0.92</td>
<td>0-4</td>
</tr>
<tr>
<td>7</td>
<td>40</td>
<td>3.09</td>
<td>1.64</td>
<td>1-7</td>
</tr>
<tr>
<td>8</td>
<td>43</td>
<td>5.84</td>
<td>1.83</td>
<td>4-10</td>
</tr>
<tr>
<td>9</td>
<td>36</td>
<td>9.33</td>
<td>2.28</td>
<td>5.5-15</td>
</tr>
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<td>10</td>
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<td>8-18</td>
</tr>
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<td>16.59</td>
<td>2.41</td>
<td>13-22</td>
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<td>12</td>
<td>33</td>
<td>21.06</td>
<td>2.59</td>
<td>17-28</td>
</tr>
<tr>
<td>13</td>
<td>26</td>
<td>25.38</td>
<td>2.42</td>
<td>22-31</td>
</tr>
<tr>
<td>14</td>
<td>26</td>
<td>30.85</td>
<td>2.87</td>
<td>26-37</td>
</tr>
<tr>
<td>15</td>
<td>20</td>
<td>34.05</td>
<td>1.79</td>
<td>32-38</td>
</tr>
<tr>
<td>16</td>
<td>8</td>
<td>39.13</td>
<td>3.64</td>
<td>36-46</td>
</tr>
</tbody>
</table>

decks exist only a short time after attaining full length before they are replaced during an incomplete first prebasic molt. The longer decks of adult-plumaged jays versus 6-12-month-old birds are new feathers, the decks of the first basic plumage having been replaced during the complete second prebasic molt.

Beak and foot.—The beak of Florida Scrub Jays is little more than half full size at fledging (Table 2), and continues to grow for almost 2 months after hatching (Table 3). As the measurement taken includes both the integumentary rhinotheca and the premaxillary bones, the increase in length shown between ages 3–4 months and 6–12 months may merely reflect changes in the rhinotheca. Feeding independence is a slow, gradual process in Florida Scrub Jays, which is not fully attained for about 3 months after fledging. Perhaps this behavior reflects the slow growth of the feeding organ.

The tarsometatarsus grows rapidly (Table 2) and attains 94% adult length at fledging (Table 3). Within a few days post fledging Florida Scrub Jays escape predators by scurrying off beneath the brush. The rapid development of the leg probably accommodates this behavior. The measurements summarized in Table 3 suggest continued slow growth of the tarsometatarsus for many months or even a year post fledging, which, if real, probably reflects lengthening of the bone and not changes in the integument.

I did not measure wings of live nestlings; however, 4 specimens, age 10
Table 2

<table>
<thead>
<tr>
<th>Age in days</th>
<th>Beak</th>
<th>Tarsus</th>
</tr>
</thead>
<tbody>
<tr>
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<td>S.D.</td>
</tr>
<tr>
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<td>49</td>
<td>3.00</td>
</tr>
<tr>
<td>1</td>
<td>55</td>
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<td>26</td>
<td>8.60</td>
</tr>
<tr>
<td>15</td>
<td>20</td>
<td>8.85</td>
</tr>
<tr>
<td>16</td>
<td>8</td>
<td>9.69</td>
</tr>
</tbody>
</table>

days, have carpometacarpi that average 71% adult length. Tarsometatarsi at age 10 days average a similar 74% adult length. Young Scrub Jays cannot fly for many days after leaving the nest, but this may be caused by factors other than retarded growth of wing bones, such as slow development of muscles and feathers.

Table 3

<table>
<thead>
<tr>
<th>Age in months</th>
<th>N</th>
<th>Beak from nostril</th>
<th>Tarsus</th>
<th>Primary no. 7</th>
<th>Deck</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5</td>
<td>20</td>
<td>**8.9 ± 0.56(^a)</td>
<td>**35.5 ± 0.91</td>
<td>**34.1 ± 1.79</td>
<td>**10.9 ± 3.09</td>
</tr>
<tr>
<td>0.5-1</td>
<td>16</td>
<td>**9.8 ± 0.52</td>
<td>36.6 ± 1.21</td>
<td>**42.1 ± 5.60</td>
<td>**20.2 ± 7.92</td>
</tr>
<tr>
<td>1-2</td>
<td>9-13</td>
<td>15.3 ± 0.56</td>
<td>36.7 ± 1.32</td>
<td>**82.2 ± 1.77</td>
<td>124.6 ± 6.37</td>
</tr>
<tr>
<td>3-4</td>
<td>27-30</td>
<td>**15.5 ± 0.86</td>
<td>36.7 ± 1.34</td>
<td>84.8 ± 2.20</td>
<td>129.4 ± 4.93(^w)</td>
</tr>
<tr>
<td>6-12</td>
<td>10-11</td>
<td>17.0 ± 1.15</td>
<td>37.0 ± 1.52</td>
<td>**83.7 ± 2.72(^w)</td>
<td>**128.9 ± 5.58(^b)</td>
</tr>
<tr>
<td>24+</td>
<td>36-56</td>
<td>17.5 ± 0.95</td>
<td>37.7 ± 1.36</td>
<td>87.5 ± 2.86(^b)</td>
<td>134.9 ± 5.56(^b)</td>
</tr>
</tbody>
</table>

\(^a\) = means followed by 1 standard deviation.
\(^b\) = Asterisks mark each mean that is significantly different from the mean immediately beneath it (t-test).
\(^w\) = D = different feathers from those measured for previous age category.
\(^m\) = M = molt of juvenile decks begins at about age 3 months.
Weight.—The growth measurement analyzed in greatest detail is weight. As a base for comparisons the weight of adult-plumaged jays is described first. An adult-plumaged Florida Scrub Jay weighs 79.2 g (s.d. = 4.36). The 60 weights chosen for this determination are of 5 live jays of each sex for 6 bimonthly periods (Dec.-Jan., etc.). All individuals chosen were at least 2 years old and appeared to be in good health. The sample range (65.6–92.0 g) encompasses the 283 live weights available for Florida Scrub Jays 2 years old and older. Variation in weight with sex in Scrub Jays was shown by Pitelka (1951) for various of the western races, but he had only 3 weights for the Florida race. The 30 males I used to determine “adult” weight averaged 81.7 g (s.d. = 4.09, range 74.1–92.0), the females 76.7 g (s.d. = 4.25, range 65.6–84.5). The weight difference between sexes is highly significant (t = 4.67). Seasonal variation in weight of adult-plumaged jays, sexes combined, is graphed at bimonthly intervals (Fig. 2); no significant differences among the 6 samples were found.

Bent (1946) describes the color, shape, and size of Florida Scrub Jay eggs, but gives no weights. The mean size of 26 eggs laid in my study tract in 1973 and 1975 (27.5 × 20.5 mm) is similar to that for Bent’s sample of 46 eggs taken from various localities in Florida prior to 1946 (27.5 × 20.3 mm). The weights of 32 fresh eggs, all measured within 1 day after laying in 1973, averaged 5.81 g (s.d. = 0.66, range 4.1–7.1): the weights of 27 eggs in the process of hatching (not necessarily the same eggs) averaged 5.03 g (s.d. = 0.55, range 4.3–6.2). For these samples weight loss from the time of laying to the time of hatching averaged 13.3%. Eight eggs weighed when fresh and also during hatching sustained weight losses ranging from 6.8 to 18.9%, with a mean loss of 12.8%, which is similar to the 13.3% registered for the larger but less controlled sample.

According to Nice (1943:74) fresh eggs weigh 8–12% of the adult female in passerines weighing up to 135 g. Nice deleted from her summary corvids weighing over 135 g, which had lesser percentages (2.5–5%). For Florida Scrub Jays, fresh eggs weigh 7.6% of adult females. In the Piñon Jay fresh eggs (\( \bar{x} = 6.65 \)) weigh 6.4% of adults (\( \bar{x} = 103.3 \)), both sexes included (calculated from Bateman and Balda 1973). Perhaps corvid eggs tend to constitute a smaller percentage of adult weight regardless of size. Four unfed hatchlings averaged 4.19 g (range 3.6–4.5). The weight of additional unfed hatchlings was estimated by subtracting the mean weight of moist empty shells, taken from eggs that failed to hatch, from the mean weight of hatching eggs. Seven fresh empty shells averaged 0.5 g (range 0.4–0.7), and the hatching eggs averaged 5.03 g, giving an estimated average value of 4.53 g. At 78% the weight of a fresh egg (5.81 g), hatchling Florida Scrub Jays are within the range listed for certain other passerines: *Lanius ludovicianus*
Table 4

Weights of Nestling Florida Scrub Jays

<table>
<thead>
<tr>
<th>Age in days</th>
<th>N</th>
<th>Weight (g)</th>
<th></th>
<th>Age in days</th>
<th>N</th>
<th>Weight (g)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>( \bar{x} )</td>
<td>S.D.</td>
<td>Range</td>
<td></td>
<td>( \bar{x} )</td>
<td>S.D.</td>
</tr>
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<td>3.5-6.5</td>
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<td>38.22</td>
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<td>5.4-9.2</td>
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<td>41.97</td>
<td>4.86</td>
</tr>
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<td>55</td>
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<td>1.42</td>
<td>7.3-13.9</td>
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<td>16.03</td>
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<td>12.1-24.6</td>
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<td>4.87</td>
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<td>42</td>
<td>29.03</td>
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<td>21.4-35.2</td>
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<td>59.75</td>
<td>2.25</td>
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<td>46</td>
<td>32.77</td>
<td>4.11</td>
<td>24.4-40.6</td>
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</table>

73-75% (Miller 1931), *Molothrus ater* and *Quiscalus quiscula* 73% (Wetherbee and Wetherbee 1961) and *Agelaius phoeniceus* 79% (Holcomb and Twiest 1968). The 95% figure obtained for Piñon Jays is suspect as pointed out by the authors. Hatchling Florida Scrub Jays weigh 6% of an adult's weight, which also is within the range for certain other passerines at 6-8% (Nice 1943) including the Piñon Jay (Bateman and Balda 1973).

The weight data for nestlings obtained in 1973 are summarized in Table 4 and graphed in Fig. 1. The day 0 weights used were taken almost entirely from nestlings that had received food before weighing. These compilations obscure the considerable variation that exists in the number of helpers and nestlings that a given pair may have. These important variables are discussed below.

Ricklefs (1968) found that growth for 2 corvid species was best described by the logistic equation:

\[
W = \frac{A}{1 + e^{-K(t_w - t_o)}}
\]

where \( W \) is the weight of the bird in grams at the age \( t_w \) (in days), \( A \) is the asymptote of weight (g) approached by nestlings, \( e \) is the base of natural logarithms, \( K \) is a constant proportional to the specific rate of growth, and \( t_o \) is the age in days at the point of inflection on the growth curve. The procedures outlined by Ricklefs (1967) were used by Bateman and Balda (1973) and in this study with similar results. For the Florida Scrub Jay, \( A \) is 60.0 (78.9 for the Piñon Jay). The age at which half of \( A \) is attained (\( t_o \)) is 8.2 days (7.6 for the Piñon Jay). The overall growth rate index (\( K \)) for the Florida Scrub Jay (0.335) is similar to that for the Piñon Jay (0.328)
Fig. 1. Weights of nestling Florida Scrub Jays. In the diagram the single vertical line represents the range of observations, the cross line the mean, the open column 1 standard deviation, and the figure atop each vertical line the sample size. Below each mean, starting with day 1, are 2 points which represent the weights of 2 starving siblings.

and the magpie Pica pica (0.332), but larger than that for the crow Corvus brachyrhynchos (0.172), a large, slow growing passerine.

An inverse measure of the overall rate of nestling growth (K) is the time required to grow from 10% to 90% (t_{10-90}) of the asymptote (Ricklefs 1968). Based on Ricklefs' regression equation of t_{10-90} on body size, the crow grows more slowly than expected (observed = 25.5 days, expected = 21.5 days), the magpie more rapidly (observed = 13.3, expected = 17.7), the Piñon Jay essentially as expected (observed = 13.1, expected = 13.3), and the Scrub Jay slightly slower (observed = 13.1, expected= 12.3).
Fig. 2. Annual fluctuation in weights of “adult” and fledgling Florida Scrub Jays. The lines connect the bimonthly means for “adults” (upper) and fledglings (lower). The vertical bars represent 95% confidence levels. The figures denote the bimonthly sample sizes for adults (above the lines) and fledglings (below the lines). Fledglings were weighed from day of departure from the nest (left side April-May sample) through 1 year.

The ratio between the asymptote and adult weight describes development at fledging. The Florida Scrub Jay at 0.76 is similar to the Piñon Jay at 0.79 (Bateman and Balda 1973), and below the values obtained for 42 of 56 other passerines (Ricklefs 1968, Table 2, R value). Low values correlate with adult foraging and fledgling escape tactics, namely moving about on the ground in search of food and eluding predators by running. An additional factor may be the location of the nest, with early fledging of species whose
Table 5
WEIGHTS AND THE FEEDER INDEX FOR NESTLING FLORIDA SCRUB JAYS

<table>
<thead>
<tr>
<th>Age in days</th>
<th>Feeder index 0.5–1.4</th>
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<th>Feeder index 1.5–3.0</th>
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<td>S.D.</td>
<td>N</td>
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<td>39</td>
<td>4.74</td>
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<td>14</td>
<td>58.29</td>
<td>4.78</td>
<td>6</td>
</tr>
</tbody>
</table>

* and ** indicate significant differences at the .05 and .01% level, respectively.

nests are more accessible to predators. Scrub Jays do not achieve adult weight for many months post fledging (Fig. 2).

Weights of fledgling and adult-plumaged jays are plotted at bimonthly intervals for 1 year (Fig. 2). The fledgling weights include only those of jays up through 1 year of age from the 1973 and 1974 year classes. The sex of many of these fledglings was unknown, however at age 1 year the sex ratio of Florida Scrub Jays seems to be equal (Woolfenden 1975), and therefore all available weights were used.

Covariance analyses (α = 0.05) of the data graphed in Fig. 2 reveal the following relationships. Weights of “adults” from May through August–September are statistically indistinguishable from the weights of “adults” taken from October–November through the following April–May; thus all “adults” are treated as 1 unit in the comparisons with fledglings. The weights of fledglings taken from time of fledging in May through August–September are neither coincident nor parallel with the weights of fledglings taken from October–November through the following April–May, and the same is true of their relationship to the weights of all “adults.” The weights of fledglings taken from October–November through the following April–May also are non-coincident (p < 0.05) with the weights of all “adults,” but they are
### Table 6

**Weights and the Feeder Index for 130 Day 11 Nestling Florida Scrub Jays**

<table>
<thead>
<tr>
<th>Year</th>
<th>Feeder index</th>
<th>N</th>
<th>Weight (g)</th>
<th>( \bar{x} )</th>
<th>S.D.</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>1973</td>
<td>0.5–1.4</td>
<td>26</td>
<td>36.7–55.0</td>
<td>**45.98</td>
<td>5.21</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.5–3.0</td>
<td>6</td>
<td>47.1–59.0</td>
<td>52.83</td>
<td>5.16</td>
<td></td>
</tr>
<tr>
<td>1974</td>
<td>0.4–1.4</td>
<td>11</td>
<td>29.6–49.2</td>
<td>*38.95</td>
<td>7.13</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.5–2.7</td>
<td>5</td>
<td>40.6–54.5</td>
<td>48.10</td>
<td>5.05</td>
<td></td>
</tr>
<tr>
<td>1975</td>
<td>0.5–1.4</td>
<td>68</td>
<td>24.6–56.2</td>
<td>*43.49</td>
<td>7.44</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.5–2.0</td>
<td>14</td>
<td>39.4–58.4</td>
<td>48.32</td>
<td>5.22</td>
<td></td>
</tr>
</tbody>
</table>

Asterisks (*) mark each mean that is significantly different from the mean immediately beneath it (t-test).

Parallel. These analyses support the conclusion that after gaining rapidly from fledging until August–September, the young jays level off at a weight below that of "adults." Inspection of the bimonthly samples (Fig. 2) reveals that between October–November and the following April–May, fluctuations in the weights of "adults" and fledglings tend to be parallel. The only bimonthly change that is significant is for fledglings between December–January and February–March \((t = 2.36)\); however the concomitant gains and losses by the 2 age-classes suggest that the changes may be real.

In 1973 significant differences in weight existed between chicks with low (0.5–1.4) and high (1.5–3.0) feeder indexes almost daily from day 4 to day 14. Significant differences apparently occur most years as evidenced by weights of day 11 chicks for 3 consecutive years (Table 6), including 1974 when the feeder index ranged from 0.4 to 2.7 and 1975 when the range was 0.5 to 2.0. Day 11 was chosen for time of weighing because it is late enough in the nestling cycle for differences in weight to have developed, but early enough that handling the young does not cause early fledging. Day 11 also is a convenient age for banding. Few other weight data useful for comparing years were obtained, and none was analyzed.

### Mortality Factors

Though difficult to measure, starvation of nestlings seems a minor cause of death in Florida Scrub Jays. Based on once-daily or less frequent visits to nests during the 6 years 1970–1975, 33 of 342 nestlings (10%) disappeared from broods known to have had a continued existence. Such gradual attrition of broods probably includes almost all nestling starvation, but also includes deaths caused by genetic defects, diseases (including parasitism), and some
predation. Thus starvation apparently kills considerably less than 10% of Florida Scrub Jay nestlings.

As a measure of starvation relative to brood size, gradual disappearance of young was measured only from nests without helpers and with broods of different sizes. For unassisted pairs with broods of 2 (n = 11), 3 (n = 25), and 4 (n = 15) nestlings, the number of young lost from continuing broods is similar at 18, 21, and 17%, respectively. As the feeder index decreases from 1.0 to 0.5 for these unassisted pairs with 2 versus 4 nestlings, this independent analysis suggests that food provisioning for nestlings is not a factor critical to reproductive success in the Florida Scrub Jay. However, food availability probably has selected for clutch size which averages only 3.4 (Woolfenden 1973).

During 7 years of watching nests, 2 breeding attempts have produced grossly underweight broods, and both of them fledged. In 1973 an unassisted pair fledged an underweight brood of 2. The young were far below normal weight a few days after hatching and soon appeared weak and sick. Their weights are plotted separately in Fig. 1. Growth of extremities, as well as weight, were retarded. At age 15 days both young were below the minimum recorded for all 4 linear measurements taken on heavier and relatively healthy young (Tables 1 and 2), and measured as follows: primary 7, 24 and 18.5 mm, deck, 3 and 0 mm, beak, 7.5 and 7 mm, and tarsus 32 and 29 mm, and weight 41.5 g and 28.0 g, respectively. These young fledged during days 21 and 20, respectively, and the lighter weight individual in all probability died within a few days. The heavier fledgling died at age 99 days, at which time he weighed only 49.6 g. However on day 82 he weighed 73.1 g, which is almost normal for that age (see Fig. 2). A heavy helmint burden may have contributed to its death (see Kinsella 1974, specimen GEW 4804).

The male (-WWS) of this breeding pair appeared to be a poor provider who seemed to spend an inordinate amount of time perched near his nest. Three years earlier, as a semi-independent fledgling in his natal territory human occupants of a nearby cabin provided the jays with a bountiful supply of peanuts. At that time I noted that this bird rarely foraged for animal food as do other young fledglings; possibly he never gained the foraging efficiency or drive necessary for feeding young.

In 1974 a case of bigamy resulted in the fledging of a brood of 2 underweight and sickly young, both of which died within days of fledging. Details, including weights of the nestlings, are given by Woolfenden (1976).

In both these instances it seems that abnormal behavior of the breeding male resulted in failure to provide sufficient nourishment to young, even though the feeder indexes at 0.5 were not abnormally low. Under normal circumstances breeding female Scrub Jays spend a large percentage of their time
at the nest (unpubl. data), especially early in the nestling cycle. Perhaps this general tendency prevented these 2 females from leaving their nests to forage and thereby compensate for the inadequacies of their mates. The point of interest here is that even when breeders exhibit abnormal behavior resulting in grossly undernourished nestlings, fledging can occur in the absence of predation.

In his analysis of 6 passerine species, Ricklefs (1969) identified only a few causes for nestling loss other than starvation and predation. Two of these, desertion and weather, are easily identified for Florida Scrub Jays and are known to be rare. By elimination, predation accounts for about 80% of all nestling losses in the population, a percentage that is considerably higher than the 66% tallied for the other 6 species. The high rate of nestling predation sustained by Florida Scrub Jays probably selects strongly for a breeding regime that reduces such losses.

**SURVIVAL**

Previously, survival through the first year of life was compared to adult mortality (Woelfenden 1973), based on a sample of 143 young from 4 year classes (1969–1972). Now, with a sample of 269 young from 6 year classes, 1970–1975 (the 1969 sample which is small is deleted to reduce chance of bias), and many weight data, it is possible to examine survival as related to nestling weight, the feeder index, and the presence of helpers.

Table 7 summarizes information on survival to feeding independence, which virtually always is accomplished by August at age three months, for 115 of the 130 young whose weights as nestlings are shown in Table 6. No differences in survival are evident among the various weight groups. Perhaps with very large samples the lightest-weight fledglings could be shown to be faring less well, and the same might be true for the heaviest young. However, neither the Mann-Whitney U-test nor the Wilcoxon 2-sample test demonstrated significance with the present sample.

The feeder index can be used in an indirect method of comparing weight and survival. As shown in Tables 5 and 6, nestlings from families with a high feeder index (1.5–3.0) weigh more than nestlings from families with a low feeder index (0.4–1.4). Even though weights were obtained for only a small portion of the young jays that have been banded and censused, the feeder index is known for virtually all. Thus the sample of young whose post-fledging survival to independence was monitored more than doubled (115 to 267) when the feeder index was used as an indication of high or low weight. The number of year classes available for testing also increases, from 3 (1973–1975) to 6 (1970–1975). The data are arranged in Table 8, and again no cause-and-effect relationship is evident; indeed survival plotted against the
feeder index yields a straight, horizontal line. These data support the premise that weight of nestlings has little effect on their later survival. Snow (1958) came to similar conclusions from his study of Blackbirds (*Turdus merula*). A regression analysis between feeder index and weight was not made because recent field work shows that merely counting the number of jays bringing food to a nest is an oversimplification in that amount of food brought varies with age and sex of individual jays (Stallcup and Woolfenden in press).

Florida Scrub Jay helpers do help, and they do so by increasing the reproductive output of breeders, usually close kin, with whom they affiliate (Woolfenden 1975). This conclusion, based on data from 1969 through 1973, is further supported by similar analyses of unpublished data obtained in 1974.

### Table 7

**Post-fledging Survival of 115 Florida Scrub Jays Arranged by Day 11 Weight**

<table>
<thead>
<tr>
<th>Weight (g) on Day 11</th>
<th>Total fledglings</th>
<th>No. of independent young</th>
<th>Percent surviving</th>
</tr>
</thead>
<tbody>
<tr>
<td>55-60</td>
<td>6</td>
<td>2</td>
<td>33</td>
</tr>
<tr>
<td>50-54</td>
<td>24</td>
<td>13</td>
<td>54</td>
</tr>
<tr>
<td>45-49</td>
<td>42</td>
<td>21</td>
<td>50</td>
</tr>
<tr>
<td>40-44</td>
<td>22</td>
<td>9</td>
<td>41</td>
</tr>
<tr>
<td>35-39</td>
<td>10</td>
<td>6</td>
<td>60</td>
</tr>
<tr>
<td>30-34</td>
<td>6</td>
<td>3</td>
<td>50</td>
</tr>
<tr>
<td>25-29</td>
<td>5</td>
<td>2</td>
<td>40</td>
</tr>
</tbody>
</table>

### Table 8

**Post-fledging Survival of 267 Florida Scrub Jays Arranged by the Feeder Index**

<table>
<thead>
<tr>
<th>Feeder index</th>
<th>Total fledglings</th>
<th>No. of independent young</th>
<th>Percent surviving</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2.7</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2.5</td>
<td>3</td>
<td>3</td>
<td>100</td>
</tr>
<tr>
<td>2.3</td>
<td>2</td>
<td>2</td>
<td>100</td>
</tr>
<tr>
<td>2.0</td>
<td>18</td>
<td>11</td>
<td>61</td>
</tr>
<tr>
<td>1.7</td>
<td>17</td>
<td>8</td>
<td>47</td>
</tr>
<tr>
<td>1.5</td>
<td>14</td>
<td>5</td>
<td>36</td>
</tr>
<tr>
<td>1.3</td>
<td>20</td>
<td>12</td>
<td>60</td>
</tr>
<tr>
<td>1.0</td>
<td>73</td>
<td>34</td>
<td>47</td>
</tr>
<tr>
<td>0.8</td>
<td>37</td>
<td>20</td>
<td>54</td>
</tr>
<tr>
<td>0.7</td>
<td>44</td>
<td>24</td>
<td>55</td>
</tr>
<tr>
<td>0.5</td>
<td>35</td>
<td>17</td>
<td>49</td>
</tr>
</tbody>
</table>
Table 9
Post-fledging Survival of 269 Florida Scrub Jays from Families With and Without Helpers

<table>
<thead>
<tr>
<th>Helper status</th>
<th>Feeder index</th>
<th>Total nestlings</th>
<th>Percent fledglings</th>
<th>Percent independent young</th>
</tr>
</thead>
<tbody>
<tr>
<td>No helpers</td>
<td>2.0</td>
<td>6</td>
<td>50</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>1.0</td>
<td>30</td>
<td>57</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td>0.7</td>
<td>87</td>
<td>54</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td>0.7-2.0</td>
<td>123</td>
<td>54</td>
<td>49</td>
</tr>
<tr>
<td>Helpers</td>
<td>2.0</td>
<td>26</td>
<td>58</td>
<td>67</td>
</tr>
<tr>
<td></td>
<td>1.0</td>
<td>77</td>
<td>73</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>0.7</td>
<td>43</td>
<td>79</td>
<td>53</td>
</tr>
<tr>
<td></td>
<td>0.7-2.0</td>
<td>146</td>
<td>72</td>
<td>53</td>
</tr>
</tbody>
</table>

and 1975. But the help helpers provide the young has little to do with food needed and food supplied (Tables 7–8). To further substantiate this phenomenon, I stabilized the weight variable by measuring survival of young jays only in families with the same feeder index, some of which had helpers, some of which did not (Table 9), and the difference between production of fledglings by families with and without helpers is highly significant ($\chi^2 = 17.9$). Survival of fledglings to feeding independence also is greater for the young from families with helpers although the differences are significant for only 2 of the feeder index categories (2.0 and 1.0), and not for the third (0.7) or for all 3 combined.

As a separate analysis, loss of clutches was measured for pairs without and with helpers with similar results: 34% of 93 nesting attempts by families without helpers were destroyed prior to hatching, but only 23% of 120 by pairs with helpers. The difference is significant ($\chi^2 = 5.7$). As eggs do not starve, this provides further evidence in opposition to the hypothesis that food provided relative to food needed limits Florida Scrub Jay reproductive success.

A question that remains is: How do helpers help increase reproductive output if it is not by means of providing the food necessary for survival of young? In the preceding section on nestling mortality, predation was identified as the factor responsible for about 80% of all nest losses. Suspected nest predators include Fish Crows (Corvus ossifragus), possibly Blue Jays (Cyanocitta cristata), certain snakes and mammals, and Scrub Jays themselves (Woolfenden 1973, 1975). Scrub Jays have an elaborate active nest defense that includes scolding, plumage displays, mobbing, and outright attack, all of which suggest these jays are capable of dissuading certain nest predators. Thus I suggest the major way that Florida Scrub Jay helpers help is by
decreasing predation on the nests containing eggs or nestlings, and to some extent on the scattered fledglings, of the breeders with which they affiliate.

CONCLUSIONS

Growth of nestling Florida Scrub Jays seems typical of passerines their size. Minor developmental features common to both Piñon and Scrub jays, which Bateman and Balda (1973) consider adaptive for breeding during cold weather by Piñon Jays, seem adaptive for breeding in a hot sunny climate by Florida Scrub Jays. Thus dark skin pigmentation and the more rapid development of dorsal feathers than those of the venter may help shield nestlings from harmful quantities of ultraviolet light. At fledging Scrub Jay young are less developed than most passerines studied thus far (Ricklefs 1968), and although comparative data are few, post-fledging growth seems retarded, as evidenced by the failure of young to attain adult weight by the end of a year. The social organization of the population probably allows for gradual growth, and indeed it may even cause it. If an advantage exists for gradual growth, the security of a defended natal territory may permit it. As an alternative hypothesis, intrafamilial dominance hierarchies relegate fledglings to subordinate positions (Woolfenden and Fitzpatrick 1977), which may suppress their gaining weight. It remains to be established whether or not these hierarchies result in higher survival of birds of particular weights.

Most Florida Scrub Jay nests fail (Woolfenden 1973), but rarely because of desertion or weather. Starvation accounts for less than 10% of all nestling losses while predation apparently accounts for over 80%. Young fed by relatively more feeders are heavier, but weight and the feeder index do not affect post-fledging survival. However, survival to fledging is related directly to the existence of helpers (Woolfenden 1975 and Table 9). Preliminary observations indicate the amount of help helpers provide varies with sex and age; therefore more refined measures of success relative to number of helpers are omitted intentionally. It is postulated that helpers assist breeders by reducing nest predation. The possibility that group breeding results in direct advantages to the breeders and the helpers is currently under investigation.

SUMMARY

Growth of young was measured in a marked population of Florida Scrub Jays that has been censused from 1969 to the present. Data were gathered mostly in 1973 when samples ranged up to 59 nestlings, which were the reproductive efforts of 28 pairs.

Fresh eggs weigh 5.8 g, 7.6% of adult female weight, and lose about 13% of their weight during incubation. Newly hatched, unfed young weigh about 4.5 g, about 78% of a fresh egg. Based on growth curve computations, nestling growth is half completed at 8.2 days. The overall growth rate index of 0.335 is similar to that of Piñon Jays, and the young
grow only slightly slower than expected for their body size. Development at fledging lags behind most passerines thus far measured, as is true also of Piñon Jays. Florida Scrub Jays do not attain “adult” weight during the first year. Growth of certain extremities also requires many months. Fluctuations in fledgling weights parallel those of “adults” from fall to early spring.

Desertion and weather rarely cause nesting failure, and starvation of nestlings accounts for less than 10% of nestling losses. Predation is the major factor; it accounts for over 80% of all nestling losses.

Breeding pairs with helpers produce more young, especially fledglings, than do unassisted pairs. Nestlings fed by relatively more feeders are heavier, but survival as fledglings does not correlate with nestling weight or the feeder index. Even nestlings half normal weight at day 11 appear to survive as fledglings as well as do heavier birds. Decreasing predation, especially on nest contents, is proposed as the major way that helpers increase reproduction. Elaborate active nest defense by breeders and helpers supports the suggestion. The suspected predators they may sometimes dissuade are certain snakes, Fish Crows, Blue Jays and Scrub Jay cannibals.

ACKNOWLEDGMENTS

As is true for the earlier work, this phase of a long-term life history study was completed through the generosity and interest of Richard Archbold, Resident Director, and James N. Layne, Director of Research, of the Archbold Biological Station. Release time from teaching during Spring quarter 1973 was made possible through a Research Council Award of the University of South Florida. Additional support came from the Frank M. Chapman Memorial Fund and the St. Petersburg Audubon Society.

Susan C. White and Stephen A. Bloom provided invaluable advice on mathematical procedures and D. Bruce Barbour, Anthony R. DeGange, John W. Fitzpatrick, Jerre A. Stallecup and Chet E. Winegarner helped with the fieldwork. Ralph W. Schreiber and Susan C. White improved the manuscript. I thank all of these persons and institutions for their help. The help of the referees, D. F. Caccamise and R. E. Ricklefs, is gratefully acknowledged.

LITERATURE CITED


 REQUEST FOR ASSISTANCE

Vulture sightings.—Sightings of and information about Turkey Vultures tagged with blue or orange streamers, each with a white letter and a one or two digit number, would be appreciated. The tags are about 3" × 6" and are fastened to the patagium with a numbered cattle ear tag. Birds are tagged on either the right or left wing. The tags are on both the dorsal and ventral surfaces of the wing. Data requested include: tag number, tag on left or right wing, date, time and place of sighting, activity of the bird and its proximity to other birds. I am particularly interested in tagged birds seen mating or in the nest. An opportunity to tag nestlings of tagged birds would be invaluable. Please send sighting data to: Bird Banding Laboratory, Office of Migratory Bird Management, Fish and Wildlife Service, Laurel, MD 20811 and/or Sheila Parness Gaby, 6832 S. W. 68 St., S. Miami, FL 33143.
VERTICAL DISTRIBUTION OF BIRDS IN A LOUISIANA BOTTOMLAND HARDWOOD FOREST

JAMES G. DICKSON AND ROBERT E. NOBLE

Resources used by avian species are probably in limited supply in forest ecosystems resulting in interspecific competition, in resource partitioning, and in the segregation of species on habitat gradients (Koplin and Hoffman 1968, Cody 1974, Schoener 1974). Resource partitioning has been accomplished through various "coexistence mechanisms" (Cody 1974). Schoener (1974) hypothesized that habitat dimensions are important more often than food-type dimensions which are more important than temporal dimensions in resource partitioning. One of these mechanisms or dimensions is a spatial segregation of birds into vertical strata. Vertical height distribution is one dimension of niche definition. MacArthur and MacArthur (1961) correlated vegetative height diversity and bird species diversity showing how bird communities responded to vegetative profiles. Tramer (1969) also noted the response of bird populations to vegetative layering. Cody (1968) observed vertical feeding height selectivity in tall vegetation, and Pearson (1971) and Karr (1971) documented vertical stratification in tropical birds.

How does maturity of an ecosystem affect bird populations and resource use? Odum (1969) predicted an increase in potential niches and interspecific competition resulting from increased biomass stratification with the advance of vegetative succession.

Another question that remains essentially unanswered is what are the seasonal patterns of resource partitioning in communities. Bird energy budgets fluctuate seasonally (King 1974) as do behavior patterns. Deciduous forests present seasonally changing vegetative profiles and habitat structures. These seasonal phenomena result in changes in bird spatial distributions.

The objective of our investigation was to ascertain vertical distributions of certain avian species and to analyze the seasonal changes in these distributions in a mature Louisiana bottomland hardwood forest.

STUDY AREA AND METHODS

This investigation was conducted on the Thistlethwaite Wildlife Management Area between Washington and Laboue, St. Landry Parish, Louisiana. The area is an old floodplain of the Mississippi and Red rivers. It is described as a south central Louisiana mature bottomland hardwood forest, and classified as hardwood bottom (Braun 1950:293). Vegetation on the area was measured on variable radii plots. The mature bottomland hardwood forest was fully stocked (-28.2 m² basal area/ha). Oaks (Quercus spp.) were dominant overstory vegetation. Cane (Arundinaria gigantea), palmetto (Sabal minor), and ironwood (Carpinus caroliniana) were primary understory species.
Vertical height data from 4103 sightings of 26 species of birds were analyzed. Height data were collected approximately 5 mornings per month from January 1972 to February 1974 while censusing birds from a 1.6 km transect. Sightings were made from sunrise to 4 h after sunrise; therefore, no data on daily patterns in heights were gathered. Vertical strata categories (MacArthur and MacArthur 1961) were: ground-0.6 m, 0.6-7.6 m, 7.6 m-canopy top (approximately 25.9 m), and above-canopy. These zones probably corresponded, as well as any, to the vegetation profile, although no distinct layers of vegetation were observable. No corrections were applied to compensate for differences in sighting distances in foliage profile throughout the year, although there were decided seasonal changes. In summer the vegetation appeared to be almost equally distributed at different heights. In winter after the deciduous leaves had fallen, the ground and mid-story vegetation, mainly palmetto and cane (both evergreen), was denser than the mostly leafless canopy.

Singing birds were omitted in this study. Sightings were not restricted to any particular behavioral category, although most birds were foraging when detected. There may have been some height differences corresponding to different bird behavior, but we did not attempt to distinguish behavior when recording heights. A behavioral division of height classes would have reduced our sample sizes significantly. We do not believe this lumping significantly affected results.

Birds were categorized into 1 of the 4 strata at the time of initial sighting with a few minor exceptions (Table 1). Ground occupants were often first seen in mid-air after having been flushed from the ground. These instances of flushing were regarded as ground sightings.

Height diversities were calculated from the information theory of Shannon (1948). Using this formula, dispersal among classes, or diversity, was calculated, based on equality of distribution of observations among the 3 classes (above-canopy stratum excluded). Height diversity = -\( \sum p_i \log p_i \), where \( p_i \) = proportion of observations in the \( i \)th category. For the 3 height categories used, 1.099 would represent maximum diversity or equal dispersal among all categories, and conversely, a complete distribution in only 1 category would have zero diversity.

Birds in the “above-canopy” stratum were divided into 2 groups: those carrying on their “normal” activities at that height and those merely relocating themselves. We included the above-canopy stratum for Black Vultures and Common Crows (Table 1) because they appeared to regularly use that height while carrying on their “normal” activities. Those relocating themselves in the “above-canopy” stratum were omitted from further consideration.

Bird vertical stratifications were compared on a seasonal, species, and family basis. The 3 strata comparisons within the forest were used for all species except the Black Vulture and Common Crow. Comparisons were tested by means of the chi square test for independent samples at the .01 level of significance unless otherwise specified. There were 2 degrees of freedom in each chi square test of 3 vertical strata. The basic assumption of this test is that all observations were independent of all other observations. We felt that data on Common Grackles and Cedar Waxwings did not meet the basic assumption, due to their occurrence in flocks and to our influence on their vertical distribution. As a result, they were excluded from further consideration. Flocking was observed to a lesser degree in other bird groups but not to the extent to invalidate the assumption of independence. The criterion for sufficient samples for reliability was taken from Siegel (1956). In comparing the 3 vertical strata within the forest, no expected
Table 1

Vertical Stratal Index of Common Thistlethwaite Birds Based on Frequency of Occurrence in 3 Strata¹

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Index²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black Vulture</td>
<td>(Coragyps atratus)</td>
<td>3.50</td>
</tr>
<tr>
<td>Common Crow</td>
<td>(Corvus brachyrhynchos)</td>
<td>3.04</td>
</tr>
<tr>
<td>Red-headed Woodpecker</td>
<td>(Melanerpes erythrocephalus)</td>
<td>2.80</td>
</tr>
<tr>
<td>Blue Jay</td>
<td>(Cyanocitta cristata)</td>
<td>2.75</td>
</tr>
<tr>
<td>Pileated Woodpecker</td>
<td>(Dryocopus pileatus)</td>
<td>2.74</td>
</tr>
<tr>
<td>Carolina Chickadee</td>
<td>(Parus carolinensis)</td>
<td>2.67</td>
</tr>
<tr>
<td>Red-bellied Woodpecker</td>
<td>(Melanerpes carolinus)</td>
<td>2.66</td>
</tr>
<tr>
<td>Tufted Titmouse</td>
<td>(Parus bicolor)</td>
<td>2.51</td>
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<tr>
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<td>(Wilsonia citrina)</td>
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<td>(Mimus polyglottos)</td>
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<td>White-throated Sparrow</td>
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∑ 38.88
\[ \bar{X} = 2.26 \]

¹ Fourth stratum (above canopy) used only for Black Vulture and Common Crow.

² Index was computed by multiplying number of sightings in each stratum by: 1 for stratum 1 (ground–0.6 m), 2 for stratum 2 (0.6–7.6 m), and 3 for stratum 3 (7.6 m–canopy top). The sum of these products for each species was then divided by total sightings, giving relative mean height.

values of less than 1 were tolerable, and no more than 20% of the expected values could be less than 5. In the few instances of a low value in 1 stratum, strata were combined for purposes of comparison.

For comparative purposes, the strata were assigned the following values: ground, 1; mid-story, 2; canopy, 3; and above-canopy, 4. Stratal index was calculated by multiplying these values in each stratum by the frequency in each stratum. The sum of these products divided by total frequency defined stratal index, based on frequency of observations in each of the strata.
Table 2

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<td>Tufted Titmouse</td>
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<td>Rufous-sided Towhee</td>
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</table>

\[ \Sigma 18.832 \]
\[ \bar{X} .785 \]

*Computed by information theory (height diversity = \(- \sum P_i \log_e P_i\), where \(P_i = \text{proportion of observations in the } i\text{th height category})

\(^2\)Equal distribution in all height categories, height diversity = 1.099; distribution in only 1 height category, height diversity = 0.

RESULTS AND DISCUSSION

Species and families.—Black Vultures had the highest mean vertical distribution (Table 1). Over \(\frac{2}{3}\) of the sightings were of soaring birds above the canopy.

Woodpeckers were predominately canopy dwellers, but different niche breadths in vertical distributions were evident. Of all sightings, 68% were above 7.6 m and less than 3% were found near the ground (Fig. 1). Pileated and Red-bellied woodpeckers were similar in vertical distribution to the aggregate of woodpeckers. Distributions of 3 species differed from the 2 above species. Common Flickers were more ground oriented (21% of sightings), and were exceeded in vertical dispersion (diversity index (DI) = 1.056, Table 2) by only one bird. Yellow-bellied Sapsuckers were primarily mid-story occupants (58%), and secondarily canopy occupants (41% of sightings) during their winter presence (DI = 0.762). Red-headed Woodpeckers were the most canopy dependent Picidae (32%) with the most restrictive vertical height dimension of niche breadth of all birds (DI = 0.513, Table 2).

The corvids were located high in the Thistletwaite woods (Table 1). Blue Jays were closely associated with the canopy level (stratal index = 2.75, DI =
0.604). They were even more strongly canopy oriented than were the Picidae ($\chi^2 = 12.6, P < .01$). Common Crows were located even higher; 40% above the tree tops.

The similarly distributed (P > .01) Tufted Titmouse and Carolina Chickadee were common canopy occupants. Fifty-four % of the Tufted Titmice and 67% of the Carolina Chickadees were observed in the canopy. They were less frequently observed in the mid-story (43% titmice, 33% chickadees). The Paridae, along with the Picidae, were the least frequent ground level occupants (titmice 3%; chickadees, none).

We sighted 83% of the Carolina Wrens in the mid-story. The chi square value for the comparison of wrens to the aggregate of all birds (which was also most numerous in mid-story sightings) was 128.6 (P < .01). Supporting this idea of mid-story association is the low height diversity of .571.

The Mimidae, Northern Mockingbirds and Brown Thrashers, were a vertically diverse group (DI = 0.898, Northern Mockingbirds; DI = 1.006, Brown Thrashers), tending toward the mid-story level. Over 50% of the sightings of each were in this level.

The tyrant flycatchers exhibited an unusual pattern of height distributions. Although we assumed that intrusion into the woods had no influence on bird heights, we may have had some effect on the heights at which Hermit Thrushes and American Robins were observed. Half of the Hermit Thrush sightings were in the mid-story and over ½ on the ground (Fig. 1). Perhaps a small portion of the mid-story sightings were of birds that flew there from the ground after being flushed. The robin was the most uniformly distributed bird in the 3 strata (DI = 1.075): ground (41%), canopy (35%), and mid-story (24%).

Ruby-crowned Kinglets were common mid-story winter residents. Of 73 sight tallies, 76% were within the 0.6–7.6 m level. The ground stratum was of little importance (5%) and the canopy stratum was of medium importance (19%). Their dispersal among the 3 strata was 0.678, near the mean of all species (0.785).

White-eyed Vireos were the only breeding vireo commonly seen. These birds were closely associated with the mid-story. This is shown by the proportion of mid-story sightings (82%) and the low height diversity (0.534, second lowest of all birds). Although there were insufficient sightings of Red-eyed and Yellow-throated vireos (V. olivaceus and V. flavifrons) for valid conclusions, the few that were sighted, and those heard, showed a canopy preference.

Yellow-rumped Warblers, 1 of 2 common winter warblers, were located mainly in mid-story (54%) and canopy (40%). The 2 commonly seen breeding season warblers, Kentucky Warbler and Hooded Warbler were selective
### SPECIES AND NO. OF SIGHTINGS

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<td>Black Vulture*</td>
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### PER CENT OF SIGHTINGS

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<td>0-0.6m.</td>
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<td>0.6-7.6m.</td>
</tr>
<tr>
<td>7.6m. - Canopy Top</td>
</tr>
<tr>
<td>Above Canopy</td>
</tr>
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</table>
in their forest profile use. Over 75% of sightings of Kentucky and Hooded warblers were in the 0.6–7.6 m stratum and the height diversity of each was less than the mean of all birds by more than 25%. They appeared to differ in use of the ground stratum (4 of 24 sightings—Kentucky Warblers, 0 of 17 sightings—Hooded Warblers), although there were insufficient data for a valid statistical test.

Brown-headed Cowbirds were mainly a mid-story, and secondarily a canopy occupant ($DI = 0.924$). Rusty Blackbirds were diversely distributed ($DI = 1.051, 34\%$ higher than the mean for all birds): they were found on the ground, mid-story, and canopy in decreasing order of occurrence.

The seed-eating fringillids, as expected, tended to be close to the ground. The 2 species (White-throated Sparrow and Rufous-sided Towhee) found most frequently near the ground were in this family. Over 75% of the White-throated Sparrows and 62% of the Rufous-sided Towhees were detected within 0.6 m of the ground. Conversely, only 3% of the sparrows and 4% of the towhees were detected in the tree canopies. The Northern Cardinal and the less common American Goldfinch differed ($P < .01$) from other fringillids. Both were mainly located in mid-story (60%, cardinal; 52%, goldfinch), and both showed high dispersal within the 3 strata ($DI > 20\%$ higher than the mean of all species).

Most individual species were more specialized than the aggregate of all birds. Of the different species investigated, only Brown-headed Cowbirds, American Goldfinches, Hermit Thrushes, and Northern Mockingbirds did not differ significantly ($P > .05$) in height distribution from sightings of all birds. These species were commonly found in all strata and as a result, exhibited a greater than average height diversity.

Vertical resource partitioning.—Different vertical resource use strategies were evident in birds in this mature ecosystem. Some species were specialists in using 1 of the 3 strata; some used 2 strata exclusively, or nearly so; some were found in all strata, but preferred 1 or 2 strata; and some species used all strata almost equally. Specialist species (i.e., those with lowest DI and $>78\%$ of sightings in 1 stratum) in the 7.6 m–canopy top stratum were Pileated Woodpecker, Red-headed Woodpecker, and Blue Jay. Carolina Wrens, White-eyed Vireos, and Kentucky Warblers were mid-story associated species, and no species were predominantly ground dwellers.

Other species concentrated their activities in 2 strata ($>94\%$ of sightings). Those found predominantly in the mid-story/canopy were: Red-bellied Woodpecker, Yellow-bellied Sapsucker, Carolina Chickadee, Tufted Titmouse, Ruby-crowned Kinglet, and Hooded Warbler. White-throated Sparrows and Rufous-sided Towhees were the ground/mid-story dwellers.

Northern Mockingbird, Brown Thrasher, Hermit Thrush, Yellow-rumped
Warbler, Brown-headed Cowbird, and Northern Cardinal were basically generalists in vertical selectivity, but showed slight preferences for 1 or 2 strata. Common Flicker, American Robin, American Goldfinch, and Rusty Blackbird were generalists in vertical distribution, displaying optimum height dispersal among the 3 strata, and maximum niche breadth.

The aggregate heights of all birds revealed a fairly uniform use of the 3 strata (Fig. 2). Each stratum was of approximate equal value as an avian resource unit. This substantiated the height units selected, and pointed out the scaling differential of birds in vertical distribution (Cody 1974:70). Although the canopy stratum represented 71% of the total forest height, only 33% of bird sightings were within this stratum. Conversely, the 0–0.6 m ground stratum represented 2% of the total height and contained 31% of the birds. Plant detritus, particularly mast, accumulated on the ground and this provided direct and indirect food sources for the ground foraging birds. Additionally, the solid substrate probably rendered the ground more accessible to foraging birds.

The mid-story contained proportionately more birds than the canopy, but fewer than the ground stratum. The continuous cover of evergreen cane and palmetto of the mid-story, may have influenced vertical distribution. Flying birds also appeared to prefer this height.

Seasonal vertical distribution.—Seasonal shifts in vertical distribution were evident in Thistletwaite birds. Due to the seasonal occurrence of some species, and the small number of samples of many others when categorized into seasons, we usually grouped individual species into higher taxa or on a residency status basis.

There was a gradual shift in distribution of birds upward in height through the 3 strata from the winter season through spring to summer and a pronounced downward movement from fall to winter. The comparison of winter to summer showed decided differences. Spring brought a slight, but non-significant (P > .05), shift upward in height for the aggregate of all birds, and for permanent residents when considered separately (Fig. 2). For all birds, ground detections fell from 38 to 36% and canopy detections rose from 29 to 32% from winter to spring. In the permanent resident group, ground detections fell from 27 to 20% and canopy sightings increased from 22 to 27% from winter to spring. Common fringillids (White-throated Sparrows, Rufous-sided Towhees, and Northern Cardinals), which were, in part, included in the 2 previous groupings, showed a significant (P < .05) shift upward in distribution from winter to spring. Ground detections fell from 70 to 65%, and canopy detections increased from 4 to 7%, as the birds responded to the seasonal spring flourish of primary production of trees and the corresponding shift of available food. Birds were attracted to new vegetation
Fig. 2. Seasonal vertical distribution of Thistletwaite birds, expressed as % of sightings in 3 height categories.

growth of the deciduous forest. White-throated Sparrows and Northern Cardinals were commonly observed feeding on new buds and samaras of American elm (Ulmus americana) in March. This winter to spring height distribution shift of the common fringillids was partially responsible for the
change in height distribution of other bird groupings in which the fringillids may have been included (permanent residents and all birds).

The movement from ground to mid-story, and from mid-story to canopy, was more pronounced from spring to summer. In comparing the spring to summer distributions of all birds combined, a chi square value of 143.81 (P < .01) was noted. Ground sightings declined to 8%, mid-story sightings increased to 57%, and canopy sightings increased to 35%. The increase in stratal index of birds substantiated this upward movement. This was partially due to a species change between seasons. The departure of White-throated Sparrows from February to April lessened the lower strata detections. But the permanent residents also exhibited a significant ($\chi^2 = 8.98$, P < .05) shift upward in response to the vegetation profile change.

A highly significant difference (P < .01) was noted between winter and summer vertical height distributions for common permanent residents ($\chi^2 = 26.11$) and the aggregate of all birds ($\chi^2 = 178.78$). There was a slight change in height distribution from winter to spring, and a more pronounced change from spring to summer. The winter to summer comparison embodied these 2 lesser seasonal height distribution changes.

The summer to fall comparison showed no discernible shift in vertical distribution of Thistlethwaite birds. Ground detection percentages remained virtually unchanged for all birds and permanent residents. Figure 2 reveals a shift of about 16% of sightings of all birds from mid-story to canopy. We believe this was misleading due to the autumn arrival of numerous Red-headed Woodpeckers. This conspicuous canopy dweller inflated the number of canopy detections. A check of the common permanent residents revealed no notable change in vertical distribution from summer to fall ($\chi^2 = 0.66$, P > .05).

With the accumulation of plant detritus, particularly mast, on the ground in fall and early winter, the birds redistributed themselves at lower levels in the profile. There was a highly significant difference (P < .01) between fall and winter for all birds ($\chi^2 = 156.25$) and for permanent residents ($\chi^2 = 9.84$).

This seasonal height distribution change resulted in a corresponding change in height diversity. A Least Squares Analysis of Variance showed a highly significant difference (F = 8.37; d.f. = 2, 3; P < .01) between seasons. Height diversity approached maximum during winter (1.092) and spring (1.097). During summer and fall diversity was lower (0.890, 0.891), with birds favoring the mid-story and canopy.

**SUMMARY**

Vertical height data from 4103 sightings of 26 species of birds were analyzed in order to better understand height segregations and resource use. Height categories used were:
ground to 0.6 m, 0.6 m to 7.6 m, and 7.6 m to canopy top (approximately 25.9 m). Bird height distributions were compared by means of the chi square test for 2 independent samples. Height diversities were computed by the information theory. The most ubiquitous species in height dispersion were: American Robin, Common Flicker, Rusty Blackbird, and American Goldfinch. The species most restricted in the forest profile and the zones they inhabited were: Red-headed Woodpecker, Pileated Woodpecker and Blue Jay—canopy; White-eyed Vireo, Kentucky Warbler, and Carolina Wren—mid-story. There was a gradual upward shift in distribution of all birds from winter through spring to the summer breeding season. There was a highly significant winter to summer height distribution change from a nearly equal distribution at all levels in winter to a predominantly mid-story and canopy distribution in summer. Corresponding with this was a reduction in height diversity of the aggregate of all birds. These shifts were presumably a response of the birds to the seasonal change in foliage profile and food supply of a deciduous forest.

ACKNOWLEDGMENTS

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LITERATURE CITED


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MENT STATION, USDA FOREST SERVICE, NACOGDOCHES, TX 75961). AC-
CEPTED 31 MARCH 1976.

REQUESTS FOR ASSISTANCE

International shorebird surveys 1978.—A cooperative International Shorebird Survey
scheme has been organized by the Canadian Wildlife Service and the Manomet Bird
Observatory since 1974 to obtain information on shorebird migration and to identify and
document areas of major importance. This scheme has been highly successful, with much
very valuable information on shorebird distribution and migration coming from contribu-
tors throughout eastern Canada and the U.S.A., the Caribbean Islands, and Central and
South America. Information from the scheme will be valuable in assessing requirements
for the future protection and conservation of the birds and their habitat. It is planned
to make 1978 the fifth and final year of the project. Any observer who may be able
to participate in regular counts of shorebirds during spring and autumn migration periods,
as well as during the winter in shorebird wintering areas, is asked to contact one of the
undersigned. Occasional counts from observers visiting shorebird areas on an irregular
basis would also be most welcome. For areas in Canada: Dr. R. I. G. Morrison, Canadian
Wildlife Service, 2721 Highway 31, Ottawa, Ontario, Canada K1G 3Z7. For areas in
U.S.A., Caribbean Islands, Central and South America: Brian A. Harrington, Manomet
Bird Observatory, Manomet, MA 02345.

Shorebird color-marking.—In 1978, the Canadian Wildlife Service will be continuing
a large-scale program of banding and color-marking shorebirds in James Bay. During
the past 3 years, over 30,000 shorebirds have been captured, resulting in more than 1200
“bird days” of sightings of dyed birds ranging from eastern Canada to South America.
Much valuable information on migration routes and strategies is being obtained and ob-servers are again asked to look out for and report any color-dyed or color-banded shore-
birds that they may see. Reports should include details of species (with age if possible),
place, date, color-marks and, if possible, notes on the numbers of other shorebirds present.
For color-dyed birds, please record the color and area of the bird that was dyed. For
color bands and standard metal leg bands, please record which leg the bands were on,
whether they were above or below the “knee,” the colors involved (yellow or light blue),
and the relative position of the bands if more than one was on a leg (e.g. right lower
leg, blue over metal, etc.). All reports will be acknowledged and should be sent to:
Dr. R. I. G. Morrison, Canadian Wildlife Service, 2721 Highway 31, Ottawa, Ontario,
Canada K1G 3Z7.
AGRICULTURAL IMPACT OF A WINTER POPULATION OF BLACKBIRDS AND STARLINGS

RICHARD A. DOLBEER, PAUL P. WORONECKI, ALLEN R. STICKLEY, JR., AND STEPHEN B. WHITE

The major concentration of blackbirds and Starlings (Sturnus vulgaris) in North America occurs in the southeastern United States where an estimated 350 million Red-winged Blackbirds (Agelaius phoeniceus), Common Grackles (Quiscalus quiscula), Brown-headed Cowbirds (Molothrus ater), and Starlings congregate in winter roosts (Meanley 1971, 1975, 1977). An estimated 75–100 major (containing >1 million birds) roosts form in the southeastern states each year.

Increasing attention is being given to many of these roosts because of nuisance problems, reputed health hazards, and agricultural damage associated with them. Although considerable effort has been directed toward developing methods for reducing roosting populations (Lefebvre and Seubert 1970), field applications of such methods have met with considerable public opposition (Graham 1976). Unfortunately, little effort has been directed to ecological studies of the various roosting species during the winter months.

The objectives of this study were: (1) to document food habits, habitat preferences and use, and general feeding and roosting behavior of the various blackbird species and Starlings using a large winter roost; and (2) to undertake a preliminary survey of the impact that this large roosting population has on agriculture within a 40 km foraging radius of the roost.

STUDY AREA AND METHODS

The study area included a large concentration of blackbirds and Starlings that roosted during the winter of 1975–76 about 7 km east of Milan, Tennessee, on the Milan Army Ammunition Plant site near the Gibson-Carroll county border. The roost, bounded by highway and pastures, was in a 21-year-old, 4.5 ha loblolly pine (Pinus taeda) plantation with little understory. The birds had been roosting each winter at various sites on the ammunition plant since at least 1969. The birds foraged primarily in Gibson County. This roost has been a center of controversy since the winter of 1974-75 when the Army attempted to reduce the bird population by spraying the roost with a wetting agent (Russell 1975).

Gibson County is a leading agricultural county in western Tennessee (Hobson 1976). In 1975, over 48,000 ha were planted to soybeans; 14,000 ha to cotton; and 11,000 ha to corn. Production of wheat, historically a minor crop in the county, increased from 3200 ha in 1973 to over 8000 ha in 1975. The county had the largest hog and cattle population in western Tennessee in 1973–75, averaging about 55,000 and 50,000 head, respectively.

Population numbers and species composition.—Between 1 November 1975 and 5 March 1976, 28 estimates of numbers and 18 estimates (at least once weekly) of the species composition of blackbirds and Starlings roosting near Milan were obtained usually by 2
observers. We made population estimates by block-counting (Meanley 1965) birds in all major flight lines as they left the roost. To estimate species composition, we stood under the flight lines of departing birds in the morning or returning birds in the evening. At least 100 random binocular sightings were made for each estimate of species composition; the first bird that entered the field of view was identified and recorded.

**Bird census for habitat use.**—Five automobile routes totaling 80 km were established on secondary roads 3 to 30 km from the roost. The routes were in zones where major flight lines from the roost have traditionally occurred and where complaints of damage to crops have been most prevalent (Russell 1975).

On 24 days between 30 October and 3 March, bird censuses were conducted on these routes by 2 observers in 1 automobile starting 0.5–1 h after sunrise and ending before 15:30 (CST). The starting route and direction were randomly selected each day; the remaining routes were run in the most expeditious order. Routes were driven at 15–45 km/h. The vehicle could be stopped for up to 1 min if necessary to observe a flock of birds through binoculars. Numbers, species, composition, and associated habitat types were recorded for all observed groups of 2 or more Starlings and or blackbirds.

The 12 habitat types were: (a) pasture (includes cemeteries and unimproved pastures with broomsedge); (b) cornfields and corn stubble; (c) wheat; (d) legumes; (e) soybean fields and soybean stubble; (f) feedlots (must include feeding apparatus or closely-fenced livestock); (g) woodlots, forest, or brush; (h) buildings; (i) thoroughly plowed (little evidence of previous crop type); (j) cotton; (k) fallow (weedy fields not in cultivation or pasture previous growing season); and (l) miscellaneous.

We ran 1 to 4 habitat surveys monthly on the census routes from late October to early March to determine the relative proportions of the 12 habitat types. We recorded the habitat type on each side of the road at 0.16 km intervals. Thus, 1000 sample points were recorded for each survey.

**Food habits.**—Between 14 November and 29 February, usually once weekly, we collected 50 to 75 birds by shotgun as they settled into the roost at dusk. Each bird was identified, sexed, and weighed before stomach and esophageal contents were placed in a vial containing 5% formalin.

For the analysis of food items, the formalin solution was drained from each vial and the vial contents were placed in a drying oven (40°C) for several hours. Each sample was then placed in a Petri dish containing five 1-mm dots symmetrically placed 2 cm apart in the form of the center and end points of an “X.” The dish was shaken and stopped at random and the food item resting on or nearest each dot was recorded. This procedure was repeated 5 times per sample for a total of 25 recordings per sample. The total for each food item (corn, wheat, sorghum, weed seeds, tree fruits, and insects) was multiplied by 4 to obtain a percentage estimate based on surface area.

This food-habits analysis is biased toward foods that are difficult to digest (e.g., corn, certain weed seeds); thus, the percentage estimates obtained should be viewed in light of this limitation. In addition, birds were collected only in the evening; thus, any diurnal pattern in food selectivity was ignored. Nonetheless, we believe this analysis provides a general view of the dominant foods of the various bird species.

**Waste corn.**—Random areas of harvested cornfields in Gibson County were searched for corn at intervals during the winter to determine the amount of waste corn available to birds. In each field, 2 strips 0.75 m by 55 m were searched. All cobs and pieces of cobs bearing kernels were collected. In addition, 2 randomly-selected areas 0.75 m by 0.75 m in each strip were searched for loose kernels. These loose kernels were collected,
and together with cob samples, removed from the fields. All kernels were removed and weighed to the nearest gram. Kilograms of available corn per ha were then calculated.

Feedlots: bird censuses and observations.—On 9 days between 29 January and 2 March 1976, we censused blackbird and Starling populations at 19 to 25 cattle and hog feedlots within 40 km of the Milan roost in the main area of foraging by the roosting population. Censuses were made from 10:00 to 15:00 CST. Each lot was observed for 5-10 min and the number and species composition of blackbirds and Starlings in the lot were estimated. In addition, we made extended observations at several lots to study the feeding behavior of the various birds species.

RESULTS

Size and species composition of roosting population.—The roost formed in early November and disbanded in early March. The roosting population estimates indicated a smooth growth to a peak population of around 11 million blackbirds and Starlings in January and early February and a sudden reduction in late February (Fig. 1). The species composition remained fairly constant between November and February (Table 1) with an overall mean

Fig. 1. Estimated number of blackbirds and Starlings using roost near Milan, Tennessee, November 1975–early March 1976.
Table 1
Average Monthly Species Composition (%) of Birds at Milan, Tennessee Roost, November 1975 Through Early March 1976

<table>
<thead>
<tr>
<th>Species</th>
<th>Nov. (%)</th>
<th>Dec. (%)</th>
<th>Jan. (%)</th>
<th>Feb. (%)</th>
<th>Early March (%)</th>
<th>Mean (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common Grackle</td>
<td>70 (2.5)</td>
<td>75 (5.2)</td>
<td>63 (6.7)</td>
<td>57 (6.3)</td>
<td>47 (0.2)</td>
<td>64</td>
</tr>
<tr>
<td>Red-winged Blackbird,</td>
<td>20 (0.7)</td>
<td>15 (1.0)</td>
<td>33 (3.5)</td>
<td>34 (3.7)</td>
<td>4 (&lt;0.1)</td>
<td>27</td>
</tr>
<tr>
<td>Brown-headed Cowbird, and Rusty Blackbird Starling</td>
<td>10 (0.4)</td>
<td>10 (0.7)</td>
<td>4 (0.4)</td>
<td>9 (1.0)</td>
<td>49 (0.2)</td>
<td>9</td>
</tr>
</tbody>
</table>

1 Red-wings, cowbirds, and Rusty Blackbirds are lumped together because of our inability to distinguish during species composition estimates.
2 Values in parentheses are peak monthly population estimates ($\times 10^6$).

of 64% grackles, 27% Red-wings and cowbirds, 9% Starlings, and a trace % of Rusty Blackbirds (Euphagus carolinus). (Red-wings and cowbirds were lumped together because they were difficult to distinguish during the species composition estimates. Based on our general observations, the bird censuses along roadsides, and the species composition of birds collected for food habits, we believe that Red-wings were more numerous than cowbirds.)

Grackle populations peaked in January whereas Red-wing, cowbird, and Starling populations peaked in February (Table 1). Grackle, Red-wing, and cowbird populations decreased rapidly in late February before Starling populations dispersed.

Daily habitat use.—The number of blackbirds and Starlings seen per census

Table 2
Number of Blackbirds and Starlings Recorded and Species Composition of These Birds on Census Routes, Late October 1975 Through Early March 1976, Milan, Tennessee Area

<table>
<thead>
<tr>
<th>Month</th>
<th>No. days census run</th>
<th>Species composition of birds observed (%)</th>
<th>Avg. birds recorded per 80 km census</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Grackles Red-wings Cowbirds Starlings Rusty BB</td>
<td></td>
</tr>
<tr>
<td>Oct.</td>
<td>1</td>
<td>0</td>
<td>23</td>
</tr>
<tr>
<td>Nov.</td>
<td>12</td>
<td>82</td>
<td>8</td>
</tr>
<tr>
<td>Dec.</td>
<td>5</td>
<td>54</td>
<td>22</td>
</tr>
<tr>
<td>Jan.</td>
<td>2</td>
<td>20</td>
<td>28</td>
</tr>
<tr>
<td>Feb.</td>
<td>3</td>
<td>53</td>
<td>17</td>
</tr>
<tr>
<td>March</td>
<td>1</td>
<td>89</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>24</td>
<td>62</td>
<td>17</td>
</tr>
</tbody>
</table>
fluctuated considerably from day to day, primarily in response to weather conditions (e.g., during inclement weather more birds were usually seen). The species composition of birds seen (grackles 62%, Red-wings 17%, Starlings 16%, cowbirds 4%, Rusty Blackbirds <1%) was similar to the estimates obtained at the roost (Tables 1 and 2).

The major habitat types along the census routes were pasture (23%) and soybeans (21%) followed by woods (13%), buildings and miscellaneous (12%), and fallow (11%) (Table 3). The relative proportions of the various habitat types remained rather stable from November through February.

The various bird species had conspicuous differences in habitat use during the winter months (Table 3). The majority of grackles were seen in cornfields and woods which made up only 4% and 13% of the habitat, respectively. Red-wings were the only species commonly recorded in soybeans: 36% of the Red-wings were seen in soybeans (21% of the habitat). Red-wings also commonly used cornfields. We observed most cowbirds (65%) at feedlots which made up <1% of the habitat. Habitat types most used by Starlings were pasture (31%), feedlots (23%), and woods (11%). They were also the only species commonly seen around buildings and urban areas.

Some major changes in habitat use occurred during the winter (Fig. 2). Starling use of wheatfields declined as the winter progressed. The use of feedlots was rather constant throughout the winter for cowbirds; however, it increased for Red-wings, Starlings, and grackles as winter progressed.

Food habits and body weights.—Corn (averaging 77%) was the dominant food for grackles during each month, November through February (Table 4).
Only in November, when acorns (Quercus spp.) made up 29% of the food items, was the percentage of corn <75% for grackles. The most common weed seed found was ragweed (Ambrosia sp.). Grackles, the only species with sufficient numbers collected of both sexes to examine sex-specific food habits, had no apparent sex-specific differences.

Corn (38%) and weed seeds (36%) were the dominant foods for Red-wings (Table 4). Weed seeds commonly consumed were Johnson grass (Sorghum halepense), cocklebur (Xanthium strumarium), chickgrass (Digitaria ischaemum), dropseed (Sporobolus sp.), smartweed (Polygonum sp.), and pigweed (Amaranthus sp.).
Table 4

Percent of various food items (by surface area) in grackles, red-wings, starlings, and cowbirds collected at Milan, Tennessee roost, November 1975 through February 1976

<table>
<thead>
<tr>
<th>Food item</th>
<th>Grackles</th>
<th>Red-wings</th>
<th>Starlings</th>
<th>Cowbirds</th>
<th>CG</th>
<th>RW</th>
<th>ST</th>
<th>CB</th>
</tr>
</thead>
<tbody>
<tr>
<td>Corn</td>
<td>56 85 89 77</td>
<td>32 40 53 27</td>
<td>8 29 - 10</td>
<td>38 54 - 92</td>
<td>77 38 16 46</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wheat</td>
<td>0 0 0 0</td>
<td>T* T 0 0</td>
<td>41 5 - 11</td>
<td>0 0 - 0</td>
<td>0 T 19 0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sorghum</td>
<td>T 0 0 0</td>
<td>1 2 0 3</td>
<td>0 0 - 0</td>
<td>7 0 - 0</td>
<td>T 2 0 4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weed seeds</td>
<td>6 5 4 7</td>
<td>44 32 26 40</td>
<td>26 29 - 33</td>
<td>44 24 - 8</td>
<td>6 36 29 34</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree seeds</td>
<td>29 3 0 T 1</td>
<td>1 1 0 1</td>
<td>15 17 - 1</td>
<td>0 0 - 0</td>
<td>8 1 9 0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insects</td>
<td>1 T T 1</td>
<td>T T 0 1</td>
<td>2 2 - 6</td>
<td>0 0 - 0</td>
<td>1 T 3 0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unidentified and</td>
<td>8 7 7 15</td>
<td>22 25 21 28</td>
<td>7 18 - 39</td>
<td>11 22 - 0</td>
<td>8 23 24 16</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>miscellaneous</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of birds in</td>
<td>129 82 31 91</td>
<td>103 70 18 27</td>
<td>21 7 0 27</td>
<td>9 5 0 1</td>
<td>269 218 55 15</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Trace (<1%).
Starlings had the most cosmopolitan diet with plant seeds (29\%), wheat seeds or sprouts (19\%), corn (11\%), and tree fruits (9\%) commonly present (Table 4). Common plant seeds were sumac (*Rhus* sp.), wild grape (*Vitis* sp.), and pokeweed (*Phytolacca americana*). The tree fruits were predominantly hackberry (*Celtis* spp.). Starlings were the only species in which insects were consistently found.

Corn (54\%) and weed seeds (34\%) were the dominant foods in the small (15) sample of cowbirds collected (Table 4). Johnson grass, ragweed, and pigweed were the dominant weed seeds.

Monthly average body weights (November–February) were determined for male and female grackles and male Red-wings (Table 5). In all cases, weights were highest in January. The average weight (±1 S.E.) for 13 female Red-wings, 56 Starlings, and 9 male and 4 female cowbirds was 48.9 ± 0.4, 86.2 ± 0.9, 52.8 ± 0.6, and 40.0 ± 1.6 g, respectively.

**IMPACT ON AGRICULTURE**

Winter wheat.—A substantial part of our study was devoted to measuring the damage inflicted by Starlings and blackbirds on winter wheat in Gibson County. This study is the subject of a separate report (Stickley et al. 1977) and will be only briefly summarized here.

Forty-eight randomly selected wheatfields along the census routes were monitored during the period November through February. Two of the 33 fields planted before 13 November received bird damage (i.e., pulling up sprouting wheat). All 15 fields planted after 12 November received some damage. Seven of these 15 fields that could be assessed for damage averaged

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**Table 5**

**Average Body Weights in Grams (±1 S.E.) for Blackbirds Collected at Milan, Tennessee Roost, November 1975 Through February 1976**

<table>
<thead>
<tr>
<th>Month</th>
<th>Male Grackles</th>
<th>Female Grackles</th>
<th>Male Red-wings</th>
</tr>
</thead>
<tbody>
<tr>
<td>November</td>
<td>126.1 ± 1.0</td>
<td>100.0 ± 0.9</td>
<td>71.5 ± 0.6</td>
</tr>
<tr>
<td>(75)*</td>
<td>(54)</td>
<td></td>
<td>(98)</td>
</tr>
<tr>
<td>December</td>
<td>126.0 ± 1.7</td>
<td>101.1 ± 0.9</td>
<td>73.6 ± 0.5</td>
</tr>
<tr>
<td>(41)</td>
<td>(41)</td>
<td></td>
<td>(68)</td>
</tr>
<tr>
<td>January</td>
<td>132.3 ± 1.0</td>
<td>103.8 ± 1.5</td>
<td>79.0 ± 1.3</td>
</tr>
<tr>
<td>(17)</td>
<td>(14)</td>
<td></td>
<td>(15)</td>
</tr>
<tr>
<td>February</td>
<td>126.4 ± 1.0</td>
<td>98.8 ± 1.2</td>
<td>72.8 ± 1.2</td>
</tr>
<tr>
<td>(64)</td>
<td>(26)</td>
<td></td>
<td>(24)</td>
</tr>
</tbody>
</table>

* Sample sizes are in parentheses.
TABLE 6
SUMMARY OF BLACKBIRD AND STARLING NUMBERS AT HOG AND CATTLE FEEDLOTS CENSUSED ON 9 DAYS FROM 29 JANUARY THROUGH 2 MARCH 1976 IN GIBSON COUNTY, TENNESSEE

<table>
<thead>
<tr>
<th>Type of lot</th>
<th>Avg. no. lots censused/day</th>
<th>Avg. no. birds in lot/census</th>
<th>Avg. species composition (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hog</td>
<td>14</td>
<td>54.0 (1000) (^a)</td>
<td>Starlings: 69, Crackles: 15, Cowbirds: 12, Red-wings: 4</td>
</tr>
<tr>
<td>Cattle</td>
<td>8</td>
<td>223.0 (3000) (^a)</td>
<td>Starlings: 17, Crackles: 20, Cowbirds: 62, Red-wings: 1</td>
</tr>
</tbody>
</table>

\(^a\) Values in parentheses represent maximum number of birds estimated in a lot during a census.

about 11% of their sprouts removed by birds. Frost damage to the 15 late-planted fields averaged 25% of the sprouts destroyed. Overall, the 48 fields suffered an estimated 3.5% sprout removal by birds and 13.5% sprout destruction by frost. Almost no fresh damage was noted after mid-January. A survey of some of these fields in May 1976, shortly before harvest, revealed no significant relationship between amount of bird damage in winter and number of mature heads of grain in May.

Almost all bird damage was done by Starlings (Table 4), a species that made up a minor (9%) part of the roosting population. Grackles commonly were observed feeding in wheatfields (Table 3) but they fed on items such as waste corn and weed seeds.

Corn.—Almost all corn was harvested in Gibson County by the time the roost developed in early November. Thus, the roosting population inflicted almost no damage to standing corn. However, both stomach contents (Table 4) and habitat-use censuses (Table 2) indicated that corn left in fields after harvest was an important food for blackbirds, particularly grackles. Most of this corn should be considered as waste corn, although in some fenced fields corn was used by livestock during the winter. About 17% of the cornfields along the census routes were fenced.

The estimated waste corn per ha of harvested cornfields declined significantly (\(P < 0.05\)) from an average of 245 kg/ha (moisture content of 20–25%) for 12 fields sampled in November to <10 kg/ha for 20 fields sampled in January and February. Thus, far less corn was available to foraging blackbirds late in winter compared with November.

Feedlots.—There were major differences in blackbird and Starling populations in cattle and hog feedlots (Table 6). Cattle lots had an average of 223 birds per census compared to 54 birds for hog lots. Cowbirds, making up 62% of the birds observed, were by far the predominant species at cattle lots, followed by grackles (20%) and Starlings (17%). In hog lots, Starlings, constituting 69% of the birds seen, were by far the predominant species, fol-
lowed by grackles (15%) and cowbirds (12%). Red-wings made up <5% of the birds at either cattle or hog lots. Although they were not enumerated during feedlot censuses, House Sparrows (*Passer domesticus*) were often as numerous as Starlings or blackbirds. Blackbirds and/or Starlings were present in about 75% of cattle and hog lots during the censuses.

The extended observations suggested that during midday, when the feedlot census was normally run, there was little exchange in the populations of blackbirds and Starlings associated with the feedlots. In the early morning and evening, however, there appeared to be a transfer of birds at feedlots (i.e., new flocks coming in to feed as other flocks left).

The actual loss of feed to birds was not measured; however, some behavioral information on feeding and qualitative information on feed loss was obtained. In hog lots, almost no feed was lost to birds directly from feeders because feeders were covered. Hogs commonly spilled grain out of feeders and this was a source of food for the birds. Starlings, the predominant species at hog lots, were the only birds seen perching on the hogs' backs. The major concern of hog farmers was the suspected role of the birds in the spread of disease among hog lots.

In cattle lots, the predominant feeding activities of birds were: (1) feeding on corn and other food items in cattle droppings, and (2) feeding in pastures associated with cattle-feeding operations. Cowbirds, grackles, Starlings, and House Sparrows were observed in feeding troughs (covered feeders are not used with cattle). Farmers expressed as much concern over feed contamination from bird droppings as they did over feed consumption by birds. Disease complaints were minor.

**DISCUSSION**

**Niche Differentiation of the Bird Species**

Grackles, Red-wings, cowbirds, and Starlings, although using a common roost at night, had strikingly different niches in their daily existence.

*Grackles.*—Grackles were not only the most numerous species at the roost, constituting about 64% of the birds and peaking at a population of over 6 million in January and early February; but, they also had the greatest body weight per bird. Thus, if we assume a 1:1 sex ratio, grackles, from the viewpoint of numbers, biomass, and energy consumed, had a greater impact than the other species combined on the ecosystem within the foraging range of the roosting population.

Food-habits analyses and the habitat-use censuses showed that waste corn was of primary importance to grackles. Overall, the negative impact that grackles had on agriculture appeared rather minor. Areas of conflict were: (1) use of feedlots in late winter, perhaps as a result of depleted supplies of
corn in fields; and (2) competition with livestock feeding in harvested cornfields. Grackles were the most common species observed in wheatfields; however, our food-habits data and observations indicated they fed on other foods (often corn) and not wheat. Thus, their presence in wheatfields can only be considered as beneficial. Thirty-one percent of the wheatfields had previously been in corn and many had considerable amounts of corn at the soil surface.

Red-wings.—Red-wings were the only species commonly associated with harvested soybean fields (Table 3). A primary food source for Red-wings in these fields appeared to be cocklebur, a common weed in soybeans. Corn was also an important food source for Red-wings: they were often observed with grackles feeding in corn stubble or wheatfields. Red-wings probably had the least impact on agriculture of all roosting species. They, along with grackles, increased their use of feedlots in late winter (Fig. 2), but were still a minor species at feedlots (Table 6).

Cowbirds.—Cowbirds were the least common species in the roosting population (with the exception of Rusty Blackbirds). They also had the lowest body weight per bird and, thus, the lowest total biomass. They were primarily associated with cattle, either in pastures or feedlots. Corn, both from feedlots and harvested fields, was an important food source.

Starlings.—Starlings made up 9% of the roosting population and about 8% of the biomass; they appeared to have the greatest negative impact on agriculture of all species. They inflicted almost all the damage to sprouting wheat and were by far the dominant species associated with hog lots. In addition, they were the only species commonly associated with buildings and urban areas. Starlings also used pastures and grassy areas much more than did the other species.

Of considerable interest also is the fact that many of the Starlings roosting in the mid-southern United States in winter (such as in Gibson County) are year-round residents of the region. For example, B. L. Monroe (pers. comm.) has estimated that 47% of the Starlings roosting in Kentucky in the winter remain in the state year-round. This contrasts with the vast majority of winter-roosting grackles, Red-wings, and cowbirds that are migrants from the northern United States and Canada (Fankhauser 1968, Meanley 1971, Meanley and Dolbeer 1977, Dolbeer 1978).

IMPACT OF BIRDS ON AGRICULTURE

Winter wheat.—The 48 wheatfields surveyed received an estimated 3.5% sprout removal (range 0–34%) by Starlings during the winter and 13.5% sprout destruction (range 0–50%) by frost. There was no apparent relationship between amount of bird damage in winter and number of mature heads
of grain in May. Thus, overall, bird damage to sprouting wheat appeared to be a minor problem in the winter of 1975–76. Most bird damage and all freeze-thaw damage occurred to fields planted after 12 November; therefore, a preliminary management recommendation for areas in western Tennessee, where bird damage is a problem, is that wheat should be planted before early November when possible. (Of course, additional data are needed to determine year-to-year and geographical variability before final management recommendations are made.) For reasons other than bird damage, the Tennessee Agricultural Extension Service recommends that wheat be planted before 1 November (Cobble 1974).

Feedlots.—This study documented that blackbirds and Starlings commonly used feedlots, and that the feeding behavior and species composition of the birds were different for hog and cattle lots. In both types of lots, the predominant species (Starlings or cowbirds) were species that made up a minor part of the bird population at the Milan roost. House Sparrows, which do not roost with blackbirds and Starlings and are present year round, were also commonly found at the feedlots.

Additional quantitative studies are needed to document: (1) the proportion of feed consumed by birds that represents a real loss to the farmer (Besser et al. 1968, Feare 1975). (2) the loss of feed in cattle lots due to contamination by birds, and (3) the role that birds at feedlots play in the spread of diseases. Also, more work, both extension and research, needs to be done in the area of feedlot design and in the use of toxicants and mechanical scare devices to reduce bird populations at feedlots (e.g., West 1968, Besser et al. 1967, Wright 1973).

Corn.—Standing corn received insignificant damage from the roosting population because almost all was harvested by the time the roost formed in early November. Nevertheless, waste corn was a dominant and perhaps critical food item, particularly for grackles and Red-wings. Further studies should be undertaken on the relationship of roosting populations to corn. The abundance of waste corn in fields may be the major factor allowing many of these large roosting populations to exist in their present locations throughout the winter.

CONCLUSIONS

The 4 bird species that composed the roost near Milan, Tennessee, varied considerably in their numbers, biomass, foraging behavior, food habits, and impact on agriculture. Because of this overall diversity and the complexity of the various problems the birds create, simplistic management schemes are likely to fail in solving the conflicts—they may even exacerbate them. For example, much of the nuisance, feedlot problem, and wheat damage in Gibson
County was caused by Starlings, a minor species in the roosting population. Attempts to exterminate or greatly reduce the roosting population by spraying with a wetting agent may selectively favor the Starling, a highly adaptable and prolific species that perhaps survives wetting-agent applications and low-temperature stressing better than native blackbird species (Odum and Petelka 1939, Lustick and Joseph 1977).

Long-term relief from the various conflicts most likely will require an integrated management program with a sound ecological basis. The use of bird-control chemicals at feedlots, roost dispersal and roosting habitat manipulation techniques, lethal control at certain roosts, changes in certain cultural practices in agriculture, chemical repellents, and public tolerance may all be a part of such an integrated approach. We hope that this preliminary study has contributed information that will help make such a management program a reality.

SUMMARY

Habitat preferences and use, food habits, and impact on agriculture were studied for 11 million blackbirds and Starlings roosting in Gibson County, Tennessee, in the winter of 1975–76. The roost was composed of Common Grackles (64%), Red-winged Blackbirds and Brown-headed Cowbirds (27%), Starlings (9%), and Rusty Blackbirds (<1%). The various species had strikingly different niches in their daily existence and impact on agriculture. Waste corn was of primary importance to grackles and Red-wings, which spent most of their time feeding in corn and soybean stubble and woodlots. Red-wings fed commonly on cocklebur seeds in soybean stubble. Cowbirds and Starlings commonly used pastures and feedlots. Starlings did almost all the bird damage to sprouting wheat. Starlings, a minor species in the roost, had the greatest negative impact on agriculture. Simplistic management schemes are likely to fail in solving bird-man conflicts caused by multi-species roosting populations—they may even exacerbate them. Long-term relief most likely will require an integrated management program with a sound ecological basis.

ACKNOWLEDGMENTS

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LITERATURE CITED


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BREEDING BEHAVIOR OF THE LOUISIANA HERON

JAMES A. RODGERS, JR.

Information on the breeding behavior of the Louisiana Heron (Hydranassa tricolor) lacks sufficient detail to permit comparison with other ardeids. Both Bent (1926) and Palmer (1962) summarized the available data from the literature and drew upon previously unpublished information from contributors. Other studies (i.e., Teal 1965, Jenni 1969) deal with the reproductive success or ecology. I have described the displays characteristic of the breeding period (Rodgers 1977). This paper reports on the breeding behavior and nesting ecology of the Louisiana Heron.

STUDY AREA

Most fieldwork was carried out on Grand Island, Barataria Bay, Plaquemines Parish, Louisiana. Except for a few scattered oyster shell beaches, the island is covered by 5-20 cm of water during high tide, but drains almost completely at low tide except for a few inland pools. Predominant vegetation includes black mangrove (Avicennia nitida) and cordgrass (Spartina alterniflora).

Observations were made from blinds at 2 sites. Site A was characterized by tall, dense black mangrove averaging 1.5-2 m high with little or no open cordgrass areas. Site B was characterized by numerous small, low-lying clumps scattered throughout an equal area of cordgrass. Herons were designated as to which site they occupied, for example, male A1 or B1. Most herons and ibises fed in surrounding estuarine regions of Barataria Bay. Hence, Grand Island was used by the Louisiana Heron primarily as a breeding site, though also used for roosting at other times of the year.

PLUMAGE CHANGES

Palmer (1962) described the nuptial molt in preparation for breeding by the Louisiana Heron. The soft-part color depicted in a colorplate (page 367) that accompanies the description requires some revision for the Louisiana Heron on the coast of Louisiana.

During the courtship phase of the breeding season, the bill tip was black as indicated, but the remaining ⅔ of the bill, including the orbital skin, was turquoise-cobalt (terminology of Ridgway 1912). Displaying males frequently rubbed the bill over the oil gland during preening with the result that the soft part colors became more intense. As noted by Huxley (1922), the turquoise-cobalt color was typically less intense in females. The entire iris of males was more of a magenta color; in females the inner margin of the iris around the pupil turned to rose. Leg color of both sexes was fleshy maroon.

During the incubation period, the turquoise-cobalt color changed to a mottled yellow in both sexes. The color change occurred first around the
eye, then along the rest of the bill. The sexes could then no longer be distinguished. The magenta color of the iris faded, the inner margin around the pupil becoming almost pink in both males and females. The legs became grayish-yellow.

TERRITORY

Louisiana Herons exhibited no pairing behavior outside the breeding season and behaved as solitary individuals while foraging and roosting in the colony. In February a slow 2-fold increase began in the roost population on Grand Island until the heronry swelled to breeding density. Louisiana Herons started to show soft-part breeding color and stayed longer on the island in the morning or returned earlier in the afternoon. Males began spending much time in a certain region of the island that eventually served as their territory. Occasionally a male picked up and manipulated a twig and then dropped it, or tugged on a branch. These actions marked the onset of the breeding season as the males began to set up their territories.

The male set up the territory, often built the foundation of the nest, and undertook the initial defense of the territory from both intruding males and females, as is the case in most North American ardeids (Meanley 1955, Meyerrick 1960, Palmer 1962). Early male Louisiana Herons staked out large territories with centers far apart; but, as other males began to enter the breeding cycle, the territories gradually became closer and territorial disputes over boundaries became increasingly common. Once a male had selected a site, he preened for long periods. Any disturbance in the vicinity or another Louisiana Heron flying by was viewed intently. Soon after the male had chosen a territory, he began to grasp and tug at branches around the site. A few low intensity performances of the Snap-Stretch display (Rodgers 1977) sometimes occurred between long preening sessions. The male occasionally went below the nest bush and returned with a twig that he used in the foundation of the nest. No matter how long the male displayed, the nest never got past a loosely arranged foundation stage.

Nests generally did not last until the next season so even the earliest males had to construct new foundations when setting up a territory. However, they often used the stunted and leafless area amidst the branches where a nest existed the previous season. Abandoned nests were almost always used again by a male later in the season. Nest height ranged between 0.3–1.3 m above the high water mark. The early males tended to set up a territory in the dense growth of 1.5–2 m tall mangroves, while the later males nested in the lower, more scattered mangroves.

The initial territory set up by the male Louisiana Heron ranged in size from 4 to 10 m in diameter. Between preening sessions and ever increasing Snap-
Stretch performances, the male roamed his territory, occasionally stopping to preen or display at a site other than the core display site. Initially all herons were threatened upon their approach to the territory and attacked if they did not leave. Pursuit flights were very frequent during this period of the breeding cycle. In general, an intruder was intimidated by the threat display of a resident male and proceeded no further. Once boundaries were established, the territory was recognized and seldom contested: hence aggression between neighboring males decreased with time.

As females were gradually allowed to stay on the territory and an increasing number of new males entered the heronry and began setting up their own territories, the size of the initially large territory gradually shrank. The territory reached its minimum size just after pair formation. This phenomenon is also characteristic of many other ardeids (Meanley 1955, Cottrille and Cottrille 1958, Meyerriecks 1960, 1962). If the nest of the Louisiana Heron was located in one of the low, isolated bushes, the territory sometimes shrank to include only the bush and its immediate vicinity, a diameter of 2–3 m. If the nest was situated in large, dense mangrove, the territory included all the bushtop area above the nest.

Figure 1 shows the history of one region of site A beginning on 11 March 1973, with special reference to male A1. Male A1 displayed from numerous sites, but concentrated display activities on the core mangrove bush. In the late afternoon of 14 March, male A1 paired. From this time on, both male and female participated in the defense of the territory. By 15 June, all nests contained either eggs or young nestlings, with the exception of the abandoned A6 site. Male A6 allowed a female to come onto his nest, where 1 copulation took place. Afterwards, he drove her from the nest and did not allow her back on. Male A6 never paired.

In the large heronry on Grand Island, territory establishment seemed to be staggered. Because the territory of a given pair shrank and left undefended areas, other males moved in and sometimes began displaying as close as 2 m from an incubating heron. These new males were noticeably tense during this period, exhibiting sleeking and constant head turning as they observed the surrounding heronry. With time, they began to roam the mangrove bush, displaying from any site where they would not be threatened or attacked by neighboring herons. Soon a core display site developed, which was usually the place where the nest foundation was begun.

As the courtship period progressed, male Louisiana Herons performed their Snap-Stretch and Circle Flights (Rodgers 1977) from the nest, but often could be observed moving to another site and displaying from there. If the nest or core site was located deep down in the mangrove bush, the male occasionally moved to the bushtop or out on a limb to display, making him
Fig. 1. The history of territory formation in one region of site A during 1973. During the early morning of 11 March, male A1 was alone and displayed from numerous sites designated by open circles, but concentrated display activities on the core mangrove bush designated with a solid circle. Later in the day A2 appeared. Territorial boundaries are indicated by dotted lines and were determined by mapping display sites and the locations of aggressive clashes.

more conspicuous to both roaming females and other territorial males. Territorial male Louisiana Herons oriented the head and looked in the direction of the acoustic cues produced in the Snap-Stretch. After pair formation, the female joined in the defense of the territory, a pattern typical of many other ardeids (Meyerriecks 1960, 1962, Blaker 1969). Later when the nestlings were 3 weeks and older they too defended the nest from both adult and juvenile ardeids when their parents were away.

Certain points should be brought out in regard to the shrinking effect of the male’s territory. First, a large territory at the early stage of courtship allowed more display sites and functioned to make the male more conspicuous to females wandering through the heronry. Second, a larger territory had more area from which the female could observe the displaying male without being driven off immediately (Meyerriecks 1960). Third, when the male finally accepted the female and formed a pair bond, a large territory was no longer needed. As a result, more males could come in and occupy newly uncontested areas of the heronry and the high breeding density characteristic of
this species developed. Fourth, the decrease in the territory size permitted the pair to channel their energy away from territory defense and into reproduction. Fifth, because the initial nest foundation served as the core for displaying and later as a site for raising the young, the immediate area around the nest was defended most vigorously at all times.

INTERACTIONS WITHIN THE PAIR

*Mate selection.*—There are many possible interactions between males and females during the courtship period (Fig. 2). Females at first landed on the
edge of the displaying male's territory. Showing little overt interest in the displaying male or the nest, the females at this time usually did not stop for any great length of time and seemed to be just moving through the colony. If the female moved too far into the territory of the male, he might first exhibit Twig Shaking (Rodgers 1977) or immediately drive her away as he would an intruding male. During the early part of the breeding season females generally did not return when driven away by the male. Later the persistent female would return repeatedly despite repeated threats and attacks by the male. Male Louisiana Herons during the early phase of courtship performed occasional Circle Flights and Snap-Stretches in between long periods of preening or twig manipulation (Fig. 3). The preening exhibited by males during this period was often marked by rapid, forceful, erratic movements. Later, preening movements were more relaxed. With an increase in time, the male performed a greater number of Snap-Stretches (Fig. 3).

At the approach of a female Louisiana Heron, the male generally returned to the core site to perform Snap-Stretch and Circle Flight displays. Once a female became attentive to a displaying male or his nest, she got as close as possible. At first she was thwarted in her attempts to get closer than the edge of the male's territory. Even though performing Snap-Stretches, the male at this time showed predominantly aggressive behavior. Twig Shaking was commonly observed as he threatened the female and often drove her off in pursuit flights. A persistent female was allowed to remain on the edge of the territory, only eliciting mild feather erection in the male. Continual attempts by the female eventually resulted in her getting within a short distance of the nest. During this time, the male repeatedly did Twig Shakes. He threatened the female with Upright and Forward displays (Rodgers 1977) and occasionally drove her back some distance or even off the territory. Often the female remained in view after being chased off by the male and returned onto his territory repeatedly, especially during the late stages of the courtship phase. Meyerriecks (1960) described similar behavior on the part of the female Green Heron (Butorides virescens).

The presence of a female initially increased the frequency of Snap-Stretch and Circle Flight displays, which were occasionally performed in rapid succession (Fig. 3). The maximum number of displays observed during any 1 min ($N = 8328$ min) was 5 Snap-Stretches and 3 isolated Snaps performed by male A1 with a female on the territory.

The female intently observed the male displaying, preening, and arranging twigs in the nest. Her attention seemed to be directed not only to the male, but the nest foundation if present. When the male performed the Circle Flight, the female watched the entire performance. Females were often observed jumping onto the nest while the male was engaged in the Circle Flight. Upon
Fig. 3. Shifts in the behavioral repertoire of male Louisiana Herons. Phases of the courtship period are: I, first 1/2 h of displaying; II, after first 1/2 h of displaying; III, behavior with a female present; IV, last 1/2 h before copulation. Abbreviations are: A, aggressive behavior (includes the Upright, Forward, and Twig Shake displays); BN, Bill-nibble; CF, Circle Flight; GD, Greeting display; P, preening; S, Snap; SS, Snap- Stretch; TM, twig manipulation.

Upon his return, the male always attacked the female and drove her away. Occasionally, as many as 3 females joined the male in the Circle Flight by flying after him and landing nearby when he returned to his nest. The female’s flight did not in any way resemble the initial components of the Circle Flight of the male, but the return flight was similar in posture and calls to the Greeting display phase performed by the male (see Rodgers 1977).
The female was allowed closer and closer until she was within 1–1.5 m of the nest. She attempted to get even closer and assumed the Withdrawn Crouch (Rodgers 1977). During an encounter with a threatening or attacking male, female Louisiana Herons often performed elements of the Greeting display, which appeared to function in reducing the aggressiveness of the male (Rodgers 1977). Often the male stopped his attack and temporarily joined in the performance of the Greeting display. This outcome allowed the female to hold her position or move slightly closer to the nest.

As the female assumed the Withdrawn Crouch, she frequently Bill-nibbled (Rodgers 1977). If she rose from her low-profile posture, she was attacked and driven off. When the female was on or near the edge of the nest, the male exhibited a tendency toward a reduction of Snap-Stretch and Circle Flight displaying (Fig. 3). In addition, much preening and Bill-nibbling was done by the female, with a slow increase in the frequency of Bill-nibbling by the male (Fig. 3).

Precopulatory period.—This period of courtship from the time the female is first tolerated on the nest to just before the first copulation by the potential pair was marked by a switch from aggressive to sexual behavior in the male. For long periods both male and female engaged in preening, interrupted by twig manipulation and Bill-nibbling. This appears to be typical of precopulatory behavior of most ardeids (Meanley 1955, Cottrille and Cottrille 1958, Meyerriecks 1960, 1962, Blaker 1969). The male Louisiana Heron still exhibited moderate feather erection, while at the same time Bill-nibbling became more frequent. He rarely performed the Snap-Stretch and Circle Flight displays once the female was on the nest (Fig. 3). The 2 herons often stood side by side, usually facing in opposite directions for periods up to 40 min. The female then rose out of the Withdrawn Crouch and stood with the male in the center of the nest without being attacked.

Copulation.—Soon after the female succeeded in getting onto the nest, the pair copulated either on (36 of 39 observations) or close to the nest platform or core display site. The male watched the female as she began manipulating twigs in the nest, and they both often Bill-nibbled. The female leaned forward, withdrew the head partially, and squatted. This act probably indicated to the male that she was ready to copulate. I observed no precopulatory display. The male mounted the female from the rear or the side by stepping up onto her back. Flapping his wings to maintain his balance, he squatted on her, grasping her shoulders with his toes. He also used leverage of his bill on the shoulder and neck region of the female for additional support. Meanley (1955) reported similar use of the bill by the male Little Blue Heron (Florida caerulea). Copulations ranged in duration from 8 to 11 sec (mean 9.8 sec; N = 23). No feather erection, nor any calls were noticed at any time preced-
ing, during, or immediately after copulation. Finishing copulation, the male rose and stepped off the back of the female. Copulation seemed to occur irregularly during the early phase of pair formation, though I observed copulations throughout the egg-laying period.

The length of time a male maintained a territory and engaged in courtship behavior without pairing is not accurately known. One instance recorded was the occupation of a territory by male A6 for only 4 days before abandoning it. Male A11 maintained a territory for 11 days before pairing.

Although I did not mark adult Louisiana Herons, I believe they practice seasonal monogamy. In 2 years, I observed no evidence of promiscuity once the male and female had paired, nor "rapes" as have been reported for the Little Blue Heron (Meanley 1955).

Postcopulatory period.—Immediately after the first copulation, the pair members engaged in long periods of preening, Bill-nibbling, and manipulating nest twigs. They also spent a lot of time standing side by side, facing in opposite directions. In this position, Huxley (in Bent 1926) has said they "intertwine their necks," but this is actually an illusion produced by their relative positions. The female soon began rearranging the twigs in the nest with the male looking on. Occasionally, both herons suddenly engaged in short performances of the Greeting display.

If the female left the nest after the first copulation to preen or find twigs, the male might not allow her back onto the nest. I observed 4 instances (N = 39 copulations) in which a male copulated with a female and then attacked her and drove her off or did not allow her return onto the nest after she had left it momentarily. This led to dissolution of the bond in 2 instances when the male repeatedly repulsed the female's attempts to get back on the nest.

Males under observation did not feed while courting. The presence of wandering females and intruding males may be the reason for their abstinence. Only after pair formation, with the presence of its mate to defend the territory, could the male forage without danger of losing his territory. Jenni (1969) also reported that male Louisiana Herons do not feed during the courtship period.

NEST BUILDING

The male was usually the one who went out and found twigs. Male Louisiana Herons passed these twigs to the female, who then worked them into the nest. Typically the period from the first copulation to the initiation of stick collecting was short. For example, pair A9 copulated at 11:43 and the male returned with the first twig in 11 min. Most twigs were gathered from on or very near the territory, but occasionally males brought material from greater distances. Birds would also take twigs from abandoned nests nearby.

When the male returned with a twig in his bill, the pair performed the
Greeting display (Rodgers 1977). Reaching out, the female took the twig in her bill and both engaged in additional head nodding and calling. The female then placed the twig in the nest as the male looked on. The male often Bill-nibbled while the female was inserting the twig. Initially, the male exhibited considerable feather erection while passing twigs to his new mate. This feather erection decreased as nest building continued and was limited to the crest and, to a lesser extent, the aigrettes.

The nest foundation begun by the male during the courtship period consisted of large twigs about 1 cm in diameter and 30–60 cm long \((N = 27)\). This structure sometimes had only 2 or 3 twigs. Twigs brought to the female after pair formation, while occasionally large, usually were about 0.5 cm in diameter and shorter than 30 cm \((N = 163)\). The finishing material consisted of small, flexible twigs and Spartina grass stems. The completed nest varied in width and depth, but always had a slight depression on the top surface that prevented the eggs from rolling out. I could distinguish no differences between the nests of Louisiana Herons and those of Little Blue Herons or Snowy Egrets \((\textit{Egretta thula})\) on Grand Island.

During nest building, one member of the pair was always on or near the territory. This prevented neighboring herons from stealing nest material. After the nest was completed, both sexes occasionally added twigs to the structure for repairs between periods of incubating or brooding. The interval between the first copulation and the laying of the first egg for 2 pairs of Louisiana Herons on Grand Island was 4 and 6 days. Jenni (1969) recorded periods of 4 and 5 days at Lake Alice, Florida.

**INCUBATION STAGE**

During the interval before the eggs were laid, the female spent a great amount of time squatting down on the nest, rearranging the nest twigs, and placing in new material. On Grand Island, the clutch size averaged 3.0 eggs \((\text{range } = 2–5, \text{ mode } = 3)\). Of the 99 nests examined, 22 contained two eggs, 58 three eggs, 18 four eggs, and 1 had five eggs. For Lake Alice, Jenni (1969) recorded the average clutch size for 35 nests as 4.1 eggs \((\text{range } = 3–9, \text{ mode } = 4)\). Teal (1965) reported an average of 3.1 eggs per clutch for 15 nests \((\text{range } = 2–4, \text{ mode } = 3)\) for Sapelo Island, Georgia.

After the clutch was completed, the pair was usually together only during a nest relief. Both sexes incubated. Nest reliefs were irregular and were accompanied by the Greeting display and Bill-nibbling. The returned heron usually preened or manipulated a few twigs in the nest before settling. Its mate often preened a short time on the edge of the nest before leaving to collect 1 or more twigs which were passed in a Greeting display to its mate who inserted them into the nest. Huxley \((\text{in Bent 1926})\) stated the number may be
as many as 11 twig presentations at 1 nest relief. My data indicate 2–5 presentations (mean 4.2, N = 167) are more common. Because the nests are in good condition structurally, I believe the display functions to reinforce the pair bond in these instances. Sometimes an incubating heron did not immediately rise off the nest when its mate returned, but remained sitting on the eggs. The returned heron then engaged in additional Greeting displaying and Bill-nibbling, after which the mate would rise off the nest.

The length of an incubation period varied considerably, from periods of less than 1 h to 1 recorded instance in which the partner did not come back during the daylight hours (about 06:00 to 20:30). Such long periods between changeovers were rare, and although nest reliefs were irregular, there tended to be 1 during the mid-morning, another during the mid-afternoon, and often 1 during the early evening. Incubation was most continuous in the early morning and early evening periods, when the ambient temperatures were cooler. During these periods the adult only occasionally rose off the eggs to preen, rearrange nest material, or sunbathe. During the late morning and afternoon, when the temperatures were the warmest, the Louisiana Heron often rose off the eggs. The bird rarely left the eggs unattended; usually it stood on the nest edge while preening or sunbathing. I never saw an incubating bird leave the nest to forage in nearby shallow inland pools. As the heron sat again on the eggs, it first erected the feathers of the lower breast and belly, then dropped the wings slightly, and shifted from side to side as it lowered its body onto the eggs. Mild crest erection also occurred.

Incubating Louisiana Herons were quick to rise and threaten any species of heron intruding on the territory. The area immediately around the nest was defended most vigorously. Disturbances outside the territory usually elicited only the Alert Posture (Rodgers 1977).

At pipping, the young Louisiana Heron emits high-pitched “peeping” sounds. During this time, adults looked at the eggs for long periods of time, sat, then rose again and peered at the eggs while turning the head from side to side. The adult heron later dropped pieces of eggshell out of the nest.

**BROODING AND CARE OF THE YOUNG**

Because incubation begins with the first egg, hatching is asynchronous. Until the nestlings were about 1 week old, the behavior of the adults was the same as during the incubation period, except for feeding the young. Adults brooded most intensively during the cool periods of morning and early evening. Herons commonly sunbathed while squatting on the nest or standing over and shading the nestlings.

From age 1 day to about 1 week, nestlings were fed small fish that were regurgitated by the parent onto the floor of the nest. The nestlings picked
up the fish in their bills. Similar behavior has been reported for the Little Blue Heron (Meanley 1955), Great Blue Heron, Ardea herodias (Pratt 1970), and Cattle Egret Bulbulcus ibis (Weber 1975). Afterwards the adult ate the unconsumed fish. Upon nest relief, the departing parent often fed the nestlings 1 more time.

When the young were 1–2 weeks of age, the bill, legs, and general body strength were well enough developed to allow grasping of the parent’s bill and they obtained a meal directly from the adult. The young were then fed one at a time with the adult leaning forward and extending the mandibles downward in such a manner that the dorsal surface of the upper mandible faced the offspring and was grasped. After feeding one nestling, the adult usually moved a short distance from the calling chicks before returning and feeding a second. This process was usually repeated several times. In such sessions, 1 nestling was often fed twice. Adults stood on the edge of the nest and could easily elude clamoring 1–2-week-old chicks: older young chased the parent around the nest bush. Hence, between feeding bouts the adult flew a short distance away to rest, preen, or sunbathe.

After the nestlings were 3–4 weeks old, the parents were seldom seen with the young except when feeding them. Pratt (1970) reported parent Great Blue Herons stay away after the young are 23 days old; Weber (1975) found that 14–21-day-old Cattle Egret chicks are left by themselves. Perhaps as the young Louisiana Herons got older, almost constant effort on the part of both parents was required to supply the developing juveniles with an adequate quantity of fish. Siegfried (1972) found that Cattle Egret nestling growth curves are steepest (hence high food demands), and chick mortality due to starving is highest at the time when both parents switched from alternate to simultaneous hunting regimes. Also, young Louisiana Herons at this age were old enough to defend themselves. With 4–5-week-old juveniles, the parent did not land on its nest bush but landed 2–5 m away, gave a series of “scaah” calls and waited for its offspring to come to it. During this time, the parent exhibited moderate feather erection which increased slightly as the young approached to receive food. As food was transferred directly to the juvenile, both the parent and young herons rapidly flapped their wings to maintain an upright position. After feeding its brood, the parent stepped and faced away, then reswallowed any fish that remained in its mouth.

Because parent Louisiana Herons refused to feed many begging juveniles that approached them, I suspect that they were able to recognize their young. Generally, the young 3–4 weeks old were the ones that approached nonparents for food. The older juveniles apparently learned to recognize their parents and probably by the process of habituation (in the terminology of Thorpe 1963), they learned that they would not get food from but would be at-

The parents returned at irregular times to feed their young. The number of feedings was usually 4 or 5 per day. When the juveniles were 7–8 weeks old, the parent-young bond had disintegrated and the juvenile herons were on their own. The adult pair bond dissolved at the same time as the parent-young relationship. The parents were no longer observed together at the nest, which by this time had disintegrated and fallen through the mangrove.

Commonly 1 nestling (less often 2) died in the nest. These were generally the youngest and therefore the smallest. Because they were at a physical disadvantage in competing with older, more aggressive siblings for the limited amount of food, they became emaciated and starved to death. On Grand Island during 1973, I recorded a mortality rate from egg laying to the 2-week-old age of 22.5%. Of the 34 nests, 1 contained one nestling, 15 two nestlings, 17 three nestlings, and 1 had four nestlings. Jenni (1969) calculated a mortality rate of 35.3% for 28 nests for the same nestling period. Teal (1965) reported a mortality rate of 68% from egg laying until the young were fledged. I attribute most of the nestling mortality on Grand Island to starvation of the younger nestlings. I saw no evidence of predation by raccoons (*Procyon lotor*); Boat-tailed Grackles (*Quiscalus major*) destroyed some eggs in a small region of the heronry outside my study area. Nestlings occasionally died after becoming entangled in mangrove branches during wind storms or while wandering from the nest. A factor that may have contributed to the low mortality rate on Grand Island is that the Barataria Bay estuarine marsh is rich faunistically and provides a good nutrient source throughout the breeding season (Day et al. 1973).

**SUMMARY**

Observations on the breeding behavior of the Louisiana Heron were made in a large heronry on Grand Island, Barataria Bay, Plaquemines Parish, Louisiana. Male Louisiana Herons with breeding soft-part colors set up large territories initially. The male appeared tense at first but soon began performing Snap-Stretch and Circle Flight displays. Soon after establishing a core display site, a male constructed the foundation of the nest there. During the early courtship period the male defended his territory from both intruding males and females. As additional males entered the breeding cycle and females began to move through the heronry, the size of the male's territory shrank.

At first a male threatened and chased away all females, but a persistent female was soon tolerated on the edge of the territory. The frequency of Snap-Stretch and Circle Flight displays increased with time and in the presence of the female. With time, she was allowed closer and closer to the nest. Assuming the Withdrawn Crouch, the female was finally allowed onto the nest where copulation took place within a short time. Later the female was allowed to occupy the center of the nest and began final construction.
The male brought twigs to the female on the nest as both engaged in the Greeting display and Bill-nibbling.

The first eggs appeared 4-6 days after the initial copulation. On Grand Island the average clutch size was 3.0 (range = 2-5, mode = 3, N = 99). Both sexes incubated. When one mate returned, the pair engaged in the Greeting display before the heron that was relieved flew off.

Both sexes fed the young, at first regurgitating small fish onto the floor of the nest. Nestlings 2 weeks and older fed by grasping the bill of the parent. Adults brought food to the brood 4-5 times a day. Many of the youngest nestlings died of starvation; chicks of all ages occasionally died in accidents. A mortality rate of 22.4% was recorded for nestlings on Grand Island for the period from egg laying through the second week after hatching. The parent-young bond began to break down when the juveniles were 6-7 weeks old.

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STATUS AND NUMERICAL FLUCTUATIONS OF SOME NORTH AMERICAN WADERS ALONG THE SURINAM COAST

Arie L. Spaans

Throughout the year, the muddy coast of Surinam (South America) forms a favorite haunt for large numbers of North American shorebirds (Haverschmidt 1955, 1968). This paper deals with the status, numerical fluctuations, and habitat selection of species that visit the Surinam coast regularly. Data were gathered from April 1970 through May 1973.

STUDY AREA AND METHODS

Study area.—The Surinam coast is situated on the northeastern fringe of South America at about 6° N latitude and between 54° and 57° W longitude (Fig. 1). Geographically, it forms a part of the Guiana coast, the nearly 2000 km of muddy and sandy shore of the Atlantic Ocean between the mouths of the Amazon and Orinoco rivers.

The coast of Surinam consists largely of vast tidal mud flats bordered on the higher parts by forests of black mangrove (Avicennia germinans). The flats alternate in space and time from an accretion to an erosion coast; the succession of accretion and erosion has a cyclic character. For a relatively small area along the Guyana coast, Diephuis (1966) established that such a cycle takes about 30 years. The rapid succession of accretion and erosion has resulted in a rather unstable shoreline. In a few places, the coast is fringed with a narrow sandy beach. In 1971, 66% of Surinam’s 350 km shoreline was in accretion, 24% was in erosion, 4% was stationary, while 6% was fringed with a sandy beach (P. A. Teunissen, pers. comm.).

The mud deposited along the Surinam coast originates from the Amazon. This river yearly discharges large amounts of fine sediments into the Atlantic Ocean, which are transported along the Guiana coasts by the Guiana Current. There the silt is deposited as a watery sediment, called “sling mud” (Diephuis 1966). These depositions result in the development of the tidal flats mentioned above. During exposure, the flats contain much water, and as a result, are very soft. In general, it is impossible for men to walk on them without sinking in. The flats are very rich in tanaids (Tanaidacea, Crustacea) and, during exposure, constitute a very important feeding habitat for North American waders.

Along the erosion parts of the coast, the littoral zone consists mostly of a narrow, firm, and tough bank of clay layers eroding from elder deposits. Like the narrow sandy beaches, these clay banks are less attractive for waders, having a much lower bird density than the tidal flats.

Landward, the coastal fringe is bordered by a wide zone of shallow lagoons and of brackish herbaceous swamps, broken by several low and narrow, wooded sand or shell ridges lying parallel to the coast. The large complexes of lagoons also form an important feeding habitat for waders. The lagoons are former mangrove forests in which the Avicennia has died in situ after prolonged inundation by sea water. For many years, the trunks of the dead mangroves are a dominant feature of the lagoons. After some time, the bare mud bottom of the lagoons may be covered by an herbaceous vegetation of halophytes, predominately saltwort (Batis maritima) and sea purslane (Sesuvium portulacastrum). Some lagoons have an extensive underwater vegetation of wigeon grass (Ruppia maritima).
The water level in the lagoons and the feeding possibilities for waders are highly variable depending on the amount of precipitation, the frequency of inundation by the sea, and the amount of evaporation. The brackish herbaceous swamps found behind the belt of mangroves are mainly covered by the spike rush (*Eleocharis* mutata) and other Cyperaceae. During most of the year, the water level in these swamps is too high for waders. In the long dry season, however, there are extensive shallow and muddy areas, which attract large numbers of shorebirds.

**Climate.**—Surinam has a tropical climate; throughout the year, the mean daily temperature remains between 26° and 28°C. The amount of rainfall varies seasonally. Most rain falls in April to July (long rainy season) with the least rain in September to November (long dry season). Between November and April, there is a short rainy season (December and January) and a short dry season (February and March), both with a moderate mean monthly precipitation (Meteorologische Dienst 1965). There is, however, much variation in the onset of the seasons, both between coastal and inland localities, and between years. Table 1 shows the distribution of the monthly rainfall at the mouth of the Matapicakanaal for 1961–70 and 1970–73.

**Data collection.**—To obtain a picture of the fluctuations in bird numbers, I made 6 series of regular counts:

1. From April 1971 through April 1973, the numbers of birds present during low tide at a mud flat 10 km northwest of Paramaribo, locally known as "Weg naar Zee" (= road to the sea), were counted at approximately 2 week intervals for one or more days from a fixed point near the high tide water mark. The area surveyed had the shape of an isosceles triangle with the observer placed at the apex (18°) on the shoreline while the low tide water mark formed the base. At low tide, the flat extended about 1 km seaward (i.e. height of the isosceles triangle).
Most counts were made late in the afternoon, when the sun interfered the least with observation. Occasionally, however, I made counts in the early morning. Counts were made with a 40 × 60 telescope. On most days, I made several counts between 1 h before and 1 h after low tide, from which I calculated the average numbers of birds present that day. These average numbers formed the starting point for further analyses.

2 and 3. From March 1971 through August 1972, I made counts at 2-4 week intervals in 2 lagoons near Krofajapasi, and from May 1971 through November 1972 in 2 lagoons near Motkreek. Both complexes of lagoons were situated just behind a sandy beach and received sea water during spring tides. On several counting-days during the long dry season, the lagoons near Krofajapasi were completely dry, with the result that many waders had gone to feed elsewhere. In contrast, on some days during the long rainy season, the water level was too high for most species of waders. The lagoons near Motkreek also had a highly variable water level, but since these lagoons were never completely dry, the fluctuations in bird numbers during the long dry season were less than in the lagoons near Krofajapasi. In the long rainy season, however, there were some counting-days with such a high water level that it must have had an unfavorable effect on the numbers of waders present.

The length of the route taken in the lagoons of Krofajapasi covered about 7 km, that in the lagoons near Motkreek about 3.5 km. The counts near Krofajapasi were made in the afternoon, those near Motkreek in the morning. Along both transects, waders were counted on both sides as far as they could be identified with certainty using 10 × 40 binoculars. At Krofajapasi, I also used a 40 × 60 telescope. As a result, the width of the area covered was not the same for each species, and thus interspecific comparisons could not be made.

4. From December 1970 through December 1971, at 2-4 week intervals, I counted waders around low tide along the nearly 8 km sandy beach east of Krofajapasi, locally known as “Bigi Santi” (≡ large beach). The counts were made between 06:00 and 09:00 (local time). This census included both the littoral zone, which was only some tens of meters wide, and the beach. The latter was mainly covered by ipomoea (Ipomoea pes-caprae) and sea bean (Canavalia maritima). During the long dry season, patches of the vegetation were burned. During the entire census period, the eastern end of the beach was fringed on the seaward side with a narrow, firm and tough eroding clay bank. During the first 9 months of the counting period, this bank was only a few hundred meters long, but after August 1971 it rapidly increased to 1.5 km. Since the bird density on the clay
bank differed from that on the sandy beach, the numbers of birds counted in these habitats will be given separately from September 1971 onward.

5. From March 1971 through October 1972, at Krofajapasi at 2–4 week intervals, I counted the numbers of Spotted Sandpipers (*Actitis macularia*) flying down the creek to their nightly roosts outside the mangrove swamps. Counts were made from about 17:00 until dark, which occurred between 18:20 and 19:00 depending on the time of the year.

6. From December 1970 through December 1971, Spotted Sandpipers were also counted along the nearly 6 km long Matapicakanal. This canal runs through a former plantation area, now mainly covered by mangroves. The counts were made at various times of the day, and at various tide levels.

**Presentation of the results.**—The results of the censuses are given as mean numbers per counting-day in 10 or 15 day periods. The status of each species will be given by an estimate of the maximum number present at one day during the season(s) involved. These estimates have been obtained by extrapolation of the transect counts for the entire coast, adjusted by the percentages of suitable habitat. Considering the small number of transects counted and the small area of each habitat they covered, these estimates, of course, give only a very rough picture of the numbers of birds. As an index of abundance, the following scale has been used:

- **very large numbers**—100,000 or more individuals
- **large numbers**—50,000–100,000 individuals
- **rather large numbers**—10,000–50,000 individuals
- **rather small numbers**—2500–10,000 individuals
- **small numbers**—500–2500 individuals
- **very small numbers**—1–500 individuals.

Data on the status only refer to the numbers present in the coastal area landward up to and including the *zone* of brackish herbaceous swamps. For some species, therefore, the number of birds in Surinam may be higher than the numbers mentioned here.

**RESULTS**

In the following list, an account is given of the occurrence of the species which visit the Surinam coast yearly. For each species, data on the status, habitat selection, and numerical fluctuations will be given:

**Black-bellied Plover** (*Pluvialis squatarola*).—This species is present throughout the year in rather small numbers, possibly in rather large numbers. It can be observed everywhere along the coast, both on soft or hard mud, and on sandy substrates.

Numbers of any importance were counted in the transects of Bigi Santi and Krofajapasi only. In both transects, the species was present throughout the year. In neither of the transects, however, was a clear-cut seasonal trend observed.

**American Golden Plover** (*Pluvialis dominica*).—This species is a transient in very small numbers from September through November. It is mainly a bird of dry inland areas. Along the coast, I observed the species on the sandy beach of Bigi Santi in an area where the vegetation had recently been burned.
and in parts of the lagoons near Motkreek that had dried up, between 15 September (1 bird) and 17 November (3 birds). My observation dates match rather well the period of fall migration mentioned by Haverschmidt (1969). Until now, the latest date for a fall migrant was 8 November (Haverschmidt op. cit.).

**Semipalmated Plover** (*Charadrius semipalmatus*).—This species is present throughout the year in rather large numbers. It is mainly distributed along the coast where it shows a strong preference for tidal flats and muddy lagoons.

Data on numerical fluctuations are available for the beach of Bigi Santi and for the lagoons near Krofajapasi (Fig. 2). At Bigi Santi, the species was seen throughout the year, except for a period of 2 months from mid-June through August. A pronounced peak in numbers occurred during late fall and early winter. In the lagoons near Krofajapasi, the species was observed
throughout the year with the same peak during the fall and winter periods. After December, numbers fell rapidly, both at Bigi Santi and near Krofajapasi. Since the drop in numbers coincides with the onset of the short rainy season, and hence with an enlargement of feeding areas in the lagoons, I suggest that it reflects a dispersal of birds to other feeding areas rather than a departure from Surinam.

During the spring, numbers remained low with no peak representing the passing of spring migrants. However, a small increase in numbers occurred in June. Since the increase was also noticed in other lagoons of the Krofajapasi area, I suggest that it reflects the arrival of summer visitors, probably from the South, rather than a concentration of birds that did not migrate to the North.

**Upland Sandpiper** (*Bartramia longicauda*).—Along the coast, this species is a transient in very small numbers in September and an irregular winter visitor. There, I observed it mostly on the sandy beach where the vegetation was rather open or where it had recently been burned. My sightings occurred between 1 September (2 birds) and 19 February (1 bird). Observation dates all fall within the period mentioned by Haverschmidt (1966).

**Whimbrel** (*Numenius phaeopus*).—This species is present throughout the year in rather small numbers with highest numbers from August through October. It is confined to muddy substrates along the coast.

None of the transect counts showed significant numbers. The statement on status mentioned above is based on qualitative data from outside the transects.

**Lesser Yellowlegs** (*Tringa flavipes*).—This species is a transient and winter visitor in very large numbers from mid-July through early May and a summer visitor in small to rather small numbers. The species is one of the most abundant waders on the tidal flats and in the shallow lagoons and brackish herbaceous swamps. Further inland, it is also numerous on flooded ricefields.

Data on numerical fluctuations are available for the mud flat near Weg naar Zee and for the lagoons near Motkreek and Krofajapasi (Fig. 3). Near Weg naar Zee, numbers increased from late July through mid-August, after which they remained high until early April. Near Motkreek, an increase in numbers occurred from mid-July through early August, after which they remained high until early March. Numbers then decreased rapidly. Near Krofajapasi, a moderate increase in numbers was seen in mid-July, followed by a decrease in September and an absence until mid-December. This was probably a result of poor feeding conditions there. From December through February, numbers remained moderate, followed by a peak abundance during March.

It might appear from the above data that a mass arrival of southbound transients did not occur before August. This, however, is not true. Large
numbers arrive in July but evidently, few make a stop for any length of time. This was corroborated by observations of large numbers of Lesser Yellowlegs heading eastward along the coast in the second half of that month.

On the mud flat near Weg naar Zee the highest numbers occurred from August through December (long dry season) and in the lagoons near Motkreek.
and Krofajapasi from December through March (short rainy season and short dry season). This indicates a shift from the mud flats to the lagoons with the onset of the rainy season.

The drop in numbers occurring after March near Motkreek and Krofajapasi suggests a mass departure from March onward. This was corroborated by observations of Lesser Yellowlegs departing the Motkreek lagoons on 10 March 1973. Data from mid-May through early July indicate that the species is a regular but not numerous summer visitor.

**Greater Yellowlegs** (*Tringa melanoleuca*).—This species is a transient in large numbers and a winter visitor in rather large numbers from mid-September through early May; it is a summer visitor in rather small numbers. Like the former, this species shows a strong preference for tidal flats and shallow lagoons; further inland, it is also common on flooded ricefields.

Data on numerical fluctuations are available for the mud flat near Weg naar Zee and for the lagoons near Motkreek (Fig. 4). The species was seen throughout the year in both transects with peak abundances during September–October (Weg naar Zee), in March (Weg naar Zee), and in April (Motkreek). The absence of a peak near Motkreek during the fall is somewhat puzzling. The peaks in fall and spring may coincide with the passage of southbound and northbound transients.

**Solitary Sandpiper** (*Tringa solitaria*).—This species is a transient and winter visitor in rather small numbers from late July through early May; it is possibly present in rather large numbers during the fall. Along the coast, this is mainly a bird of shallow lagoons and brackish herbaceous swamps; further inland, it is also a common visitor of freshwater pools and ditches, and of flooded ricefields.

I observed the species during the transect counts only occasionally. The statement on status mentioned above is based on qualitative data from outside the transects. My observations of a Solitary Sandpiper on 19 July 1972 and one on 9 May 1971 are the earliest and latest dates respectively, for this species in Surinam (see Haverschmidt 1968).

**Spotted Sandpiper** (*Actitis macularia*).—This species is a transient and winter visitor in rather large numbers from early July through early June; it is a summer visitor in very small, local numbers. The species is not confined to the coast and may be found everywhere that water is present. Along the coast, it shows a preference for shallow and muddy lagoons, but it may also be commonly found along creeks and canals, on firm and tough clay banks emerging from eroding coastline, and on higher parts of mud flats. During fall migration, it is also numerous on sandy beaches.
Fig. 4. Seasonal variations in numbers of Greater Yellowlegs along the Surinam coast. A. Mud flat near Weg naar Zee, April 1971 through April 1973. B. Lagoons near Mot-kreek, October 1971 through November 1972. Conventions as in Fig. 2 and 3.

Data on numerical fluctuations are available for Krofajapasi, Matapicakanal and the beach of Bigi Santi (Fig. 5). The first fall migrants arrive during early July. The earliest dates, based on records from places where the species was absent in the weeks before, are: 2 July 1971 (2 birds), 5 July 1972 (8 birds; these birds must have arrived during the night since the species was still absent the day before at each place of observation), and 6 July 1970 (1 bird). After then numbers built up rapidly, reflecting a mass arrival of migrants. From August through May, the numbers of birds flying down Krofajapasi Creek fluctuated heavily; highest numbers were in January and lowest numbers were in September. Along the Matapicakanal, the numbers remained high through January with much lower numbers occurring dur-
Fig. 5. Seasonal variations in numbers of Spotted Sandpipers along the Surinam coast. A. Krofajapasi Creek, March 1971 through October 1972. B. Matapicakanaal, December 1970 through December 1971. C. Beach of Bigi Santi, December 1970 through December 1971. Conventions as in Fig. 2.

During the spring months. At Bigi Santi, numbers decreased sharply during September, indicating that the peak of fall transients passed through mainly in August and early September. During the spring months, no migration peak was observed in any of the transects.

During June, only few Spotted Sandpipers were seen, either in or outside the transects. Of my 14 observations (25 birds) in June, 8 (18 birds) were
of birds flying down Krofajapasi Creek during the routine counts throughout the entire month. The other 6 records (7 birds) were from other places, and all fell in the first week of June. The latter, therefore, are likely to be late spring migrants rather than summer visitors. The data show, however, that near Krofajapasi Spotted Sandpipers were present during the whole month of June. I feel justified in considering these as summering birds. Only 2 June records have previously been reported (Haverschmidt 1968).

**Willet** (*Catoptrophorus semipalmatus*).—This species is a transient in rather large numbers, possibly in large numbers, from early July through mid-August; it is present during the other months in rather small numbers. The species is confined to the coast where it shows a strong preference for tidal flats. During the fall migration, however, large flocks may also be encountered in lagoons that have dried up.

Data on numerical fluctuations are only available for the mud flat near Weg naar Zee (Fig. 6). The species was seen here throughout the year with a peak abundance from late July through mid-August, after which the mean numbers fluctuated around a low level. In March (1973) and April (1972), the numbers counted were somewhat higher, perhaps reflecting the passage of small numbers of spring migrants.

From these data, it might appear that a mass arrival of southbound transients did not occur before the end of July, but this is not true. Elsewhere along the coast, the species was already numerous in mid-July. In 1972, I observed several flocks of 10–50 birds heading east at Eilanti as early as 4 July. Although peak numbers are over by late August, transients may pass until well into October.

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**Fig. 6.** Seasonal variations in numbers of Willets along the Surinam coast (mud flat near Weg naar Zee, May 1971 through April 1973). Conventions as in Fig. 2.
**Ruddy Turnstone** (*Arenaria interpres*).—This species is present throughout the year in rather large numbers. It can be found everywhere along the coastal shore where the substrate is firm.

Counts were made along the beach of Bigi Santi and in the lagoons near Krofajapasi. The numbers counted in these transects show no clear-cut seasonal trend, except for an increase during the fall and early winter on the clay bank at the eastern end of Bigi Santi coincident with an increase in the length of this bank. In neither of the two transects was there any indication of a migration peak in the northern spring. In both transects, rather fair numbers were present during the northern summer months.
Short-billed Dowitcher (*Limnodromus griseus*).—This species is a transient in very large numbers during the fall, from mid-August through early October, and during the spring, from early March through late May; it is a winter and summer visitor in small numbers. This species was found almost exclusively in lagoons and on tidal flats. On the latter, it showed a strong preference for the zone of sling mud near the low-water mark.

Data on numerical fluctuations are available for the mud flat near Weg naar Zee and for the lagoons near Motkreek (Fig. 7). Near Weg naar Zee, numbers were high from late summer through early fall and in the spring. Numbers were low during the northern winter, and the species was absent during the northern summer. Near Motkreek, highest numbers were seen in late summer and early fall, and lowest numbers were seen during the northern winter and summer. The low spring numbers probably resulted from high water levels during the long rainy season.

Red Knot (*Calidris canutus*).—This species is a transient in small numbers from mid-August through late October and in early May; it is a summer and winter visitor in very small numbers. Most Red Knots were observed on firm and tough clay banks emerging from eroding coastline and in shallow lagoons. I never observed the species on the soft tidal flats.

Since the species was not observed frequently in any of the transects all observations of knots along the coast have been lumped to obtain an idea about its occurrence (Fig. 3). The species was seen throughout the year with peaks from August through October, and in May.
**Sanderling** (*Calidris alba*).—This species is a transient and winter visitor in small, possibly in rather small numbers, with highest numbers in fall; it is a summer visitor in very small numbers. The species, confined to the coast, was almost exclusively found on sandy beaches and on firm and tough clay banks emerging from eroding coastline.

Data on numerical fluctuations are available only for the beach of Bigi Santi (Fig. 9). The species was seen throughout the year with highest numbers from September through December. On an average, the lowest numbers were seen from May through August, but in one census (17 June 1971) 33 birds were counted—almost as many as the average number during the first three months of the year. In September, there was an increase in numbers on the sandy beach. Some tens of birds were also observed then on the clay bank fringing the shore at the eastern end of the beach, where the species had not been seen in the months before. On the sandy beach, numbers remained more or less constant throughout the rest of fall, except for a peak in the second half of September. However, on the clay bank, parallel to an increase in its length, numbers increased from October onward. A pronounced migration peak in spring was not observed, but it should be noted that no data were available for April.
Fig. 10. Seasonal variations in numbers of Semipalmated Sandpipers along the Surinam coast. A. Mud flat near Weg naar Zee, April 1971 through April 1973. B. Lagoons near Krofajapasi, March 1971 through April 1972. Conventions as in Fig. 2.

**Semipalmated Sandpiper** (*Calidris pusilla*).—This species is a transient and winter visitor in very large numbers from mid-August through mid-June, and a summer visitor in rather large numbers, possibly in large numbers. The species is mainly confined to the coast, where it shows a strong preference for tidal flats and shallow lagoons.

Data on numerical fluctuations are available for the mud flat near Weg naar Zee and for the lagoons near Krofajapasi (Fig. 10). Numbers near
Weg naar Zee increased gradually starting about mid-August with peak abundance in early November, after which they decreased. During the northern winter, numbers fluctuated heavily with fewer present in January and February than in December. From late February onward, numbers were somewhat higher, with a small peak in early May. After this, numbers decreased to the low summer level.

Near Krofajapasi, no increase in numbers was observed after the onset of the fall migration. This was probably due to poor feeding possibilities there during the long dry season. After the onset of rains in January 1972, numbers were higher with peak abundance in April. Relatively high numbers were also present in June and July, when numbers near Weg naar Zee were at their lowest. This suggests that summering birds may concentrate at certain localities, which was corroborated by observations of large numbers elsewhere along the coast. For example, 30 June 1971, at least 12,000 Semipalmated Sandpipers were present on the tidal flats east of the mouth of the Coppename River, while in early July 1972, several thousand were present on the flats near Eilanti.

**Western Sandpiper** (*Calidris mauri*).—This species is a winter visitor in small numbers, possibly in rather small numbers, and probably a summer visitor in very small numbers. The Western Sandpiper is confined to the coast, where it frequents tidal flats and shallow lagoons. In western Surinam, they are probably more numerous than near Paramaribo. During 1970–73, around high tides, we caught only 2 *C. mauri* against nearly 3700 *C. pusilla* in the mangrove swamps near Weg naar Zee. In Nickerie, in the west of the country, however, Mr. W. E. van der Schot (pers. comm.) found at least 8 *C. mauri* (of which several are now in the Zoological Museum, Amsterdam) among 54 “peeps” shot by a hunter on 12 November 1972.

**Least Sandpiper** (*Calidris minutilla*).—This species is a transient and winter visitor in large numbers from mid-July through mid-June, and a summer visitor in small, local numbers. Along the coast, the species shows a preference for muddy lagoons and brackish herbaceous swamps. As far as I know, it avoids the exposed areas of the tidal flats but is rather numerous on open sites in the mangrove forests. The species is not restricted to the coast; further inland, it is a common species along ditches, in freshwater swamps, and in flooded ricefields.

Fig. 11 shows the numerical fluctuations in the lagoons near Motkreek and Krofajapasi. Near Motkreek, numbers increased during mid-July. From early August through early May, the species was present in fluctuating numbers with peak abundances in mid-August, early February, and early May. From late May through late June, the species was not observed in this transect.
Fig. 11. Seasonal variations in numbers of Least Sandpipers along the Surinam coast. A. Lagoons near Motkreek, May 1971 through November 1972. B. Lagoons near Krofajapasi, March 1971 through August 1972. Conventions as in Figs. 2 and 3.
Near Krofajapasi, numbers increased gradually from mid-July through September, after which numbers fluctuated heavily with peaks in mid-November and early April. After early May, numbers decreased, but the species was present through mid-June. In late June and early July, no Least Sandpipers were observed in this transect.

Since the peak abundances were found in different periods of the year for the two complexes of lagoons, I suggest that they reflect fluctuations in feeding opportunities in the lagoons rather than differences in abundance as a result of arrival or departure of transient birds. In both transects, no birds were observed between departure of the last spring migrants and arrival of the first fall migrants. In this period, however, the species was observed regularly near Krofajapasi outside the transects. In the second half of June and first half of July 1971 and 1972, on five different dates, a total of at least 74 Least Sandpipers was observed. From these observations it may be concluded that at least locally, the species stays over during the northern summer. Summer records have not been reported previously (Haverschmidt 1968, pers. comm.).

White-rumped Sandpiper (Calidris fuscicollis).—This species is a transient in rather large numbers from mid-August through late November and in rather small numbers from early April through mid-June; it is probably an irregular winter visitor in small or very small numbers. The species was observed almost exclusively in lagoons and brackish herbaceous swamps. As far as I know, it avoids the lower zones of tidal flats. It may occur occasionally, however, in the higher zones of the littoral. The species also occurs further inland along freshwater pools and ditches.

Fig. 12 shows the seasonal variations in numbers in the lagoons near Motkreek and Krofajapasi. There was a mass arrival during late August (earliest date, 20 August 1972) and large numbers were also encountered in September. In October and November, however, only small numbers were seen. Most fall transients therefore pass through Surinam during the last ten days of August and in September. This is corroborated by a strong easterly migration parallel to the coast during these months (e.g. 31 August 1971, when, between 09:30 and 10:30, 688 birds in 61 flocks were observed near Motkreek flying low over the ground in an easterly direction). My latest fall observation date for this species is 28 November 1971. During the spring there was a low peak in May with the first birds arriving in early April (earliest date, 8 April 1972); the last birds departed mid-June (latest date, 21 June 1972).

Fall migration started much earlier and spring migration was extended much longer than mentioned by Haverschmidt (1968). Although I was on the
look-out for wintering and summering birds, I did not locate any. Mr. F. Haverschmidt (in litt.) told me, however, that he observed the species several times in the swamps near Maasstroom in December 1963 and February 1964, suggesting that in some years the species may stay over during the northern winter.

**Pectoral Sandpiper** (*Calidris melanotos*).—In Surinam, this is more a bird of inland than of coastal habitats. Along the coast, I observed the species...
Stilt Sandpiper (Micropalama himantopus).—This species is a fall transient in rather large numbers and a winter visitor in rather small numbers from early August through mid-May; it is probably a summer visitor in small or very small numbers. The species is confined to shallow lagoons and brackish herbaceous swamps. I have no observations of this species from the tidal flats.

Fig. 13 shows the fluctuations in Stilt Sandpiper numbers in the lagoons occasionally in shallow lagoons. It is probably more numerous in the brackish herbaceous swamps, and as far as I know, it avoids the tidal flats. Because of its scarce occurrence along the coast, I am not able to add new facts about its stay in Surinam (see Haverschmidt 1968).
near Motkreek and Krofajapasi. The first fall transients arrive during early August. The two transects respectively show peak abundance in mid-August and late August, reflecting a mass influx of southbound transients during this period. From September onward, numbers decreased in both complexes of lagoons, albeit more rapidly in the lagoons near Krofajapasi than in those near Motkreek. This difference possibly resulted from deteriorating feeding conditions in the former. During the northern winter and spring, the species was present in fluctuating numbers in both complexes of lagoons. No migration peak during the spring months was observed. The presence of large numbers of Stilt Sandpipers in nuptial plumage in the first half of May 1970 and 1971, indicates that spring departure continues until mid-May. During the northern breeding season Stilt Sandpipers were counted during early June only near Krofajapasi.

CONCLUSIONS AND DISCUSSION

Occurrence.—Of the 24 species and subspecies of North American waders known to visit the Surinam coast, 20 do so regularly. Most of these are present in Surinam throughout the year (Haverschmidt 1955, and 1968; and this paper). Exceptions are the American Golden Plover, Upland Sandpiper, Solitary Sandpiper, White-rumped Sandpiper, and the Pectoral Sandpiper, species for which no summer records are known. Records of the American Golden Plover are also lacking from the northern winter.

Of the 20 regular visitors, the Lesser Yellowlegs, Short-billed Dowitcher and the Semipalmated Sandpiper occurred during the study in very large numbers (maximum numbers present at one day estimated at >100,000), the Greater Yellowlegs, Least Sandpiper, and possibly the Willet in large numbers (maximum numbers 50,000–100,000), and the Semipalmated Plover, Spotted Sandpiper, Ruddy Turnstone, White-rumped Sandpiper, and the Stilt Sandpiper in rather large numbers (maximum numbers 10,000–50,000). The remaining species, except 2, occurred in maximum numbers lower than 10,000. The exceptions are the Black-bellied Plover and the Solitary Sandpiper, which were classified as occurring in rather small, possibly in rather large numbers.

Fall migration routes.—For several species the occurrence and abundance in fall differ to some extent from those in northeastern Venezuela as reported by McNeil (1970). In Surinam, peak numbers of the American Golden Plover, Willet, Short-billed Dowitcher, Red Knot, and the White-rumped Sandpiper are reached much earlier during the fall than they are in northeastern Venezuela. For the Red Knot and the White-rumped Sandpiper, peak numbers in Surinam are also much higher than in northeastern Venezuela. These data may indicate that these species reach Surinam from North America mainly through
a non-stop flight across the Atlantic Ocean. There is much circumstantial evidence that a non-stop flight across the Atlantic Ocean in late summer and fall is a common feature among waders. Radar studies along the coast of the Canadian Atlantic provinces (Richardson 1974), Massachusetts (Drury and Keith 1962, Nisbet 1963), and New Jersey (Swinebroad 1964) have shown that large numbers of North American waders on southbound migration move out to sea in ESE-SSE directions, "... as if on a non-stop flight to northern South America" (Drury and Keith 1962). In addition, McNeil and Cadieux (1972) and Burton and McNeil (1975) working on southbound migrating waders at the Magdalen Islands in the Gulf of St. Lawrence and at Sable Island off Nova Scotia showed that many North American waders leave the Canadian Atlantic provinces with enough energy reserves to fly non-stop over the Atlantic Ocean to reach the Lesser Antilles and the northeastern coast of South America. Moreover, the regular occurrence of various species of North American waders at Bermuda in late summer and fall (Wingate in Drury and Keith 1962) also points to a transoceanic flight to South America, as do the recoveries of birds banded at the Magdalen Islands and at Sable Island (McNeil and Burton 1973, Burton and McNeil 1975).

The Greater Yellowlegs and the Semipalmated Sandpiper, on the other hand, reach their fall peak much later in Surinam than in northeastern Venezuela. For the Semipalmated Sandpiper, the Surinam peak follows a large departure of adults from Venezuela (McNeil 1970), which might indicate a relationship between counts in the two areas.

Spring migration routes.—In spring, too, some striking differences in occurrence and abundance were found between Surinam and northeastern Venezuela. In Surinam, a large spring migration peak was observed in the Short-billed Dowitcher and the Red Knot, and possibly also in the Greater Yellowlegs and the Willet, whereas in northeastern Venezuela none of these species showed a significant increase in numbers. In Venezuela, on the other hand, the Semipalmated Plover, Lesser Yellowlegs, Spotted Sandpiper, Ruddy Turnstone, Semipalmated Sandpiper, White-rumped Sandpiper, Stilt Sandpiper, and possibly the Least Sandpiper did show a clear spring migration peak, whereas in Surinam no migration peak, or only a very small one, was observed in these species.

On the basis of these data, I suggest that the spring migration route of Short-billed Dowitches and Red Knots, and possibly also of Greater Yellowlegs and Willets, wintering south of the Guianas, is mainly to the Guiana coast, and from there non-stop across the Atlantic Ocean to North America. The latter suggestion is supported by observations of the departure of several flocks of Short-billed Dowitches near Weg naar Zee in late April and early May 1971 and 1972, in directions varying between 332° and 351° (Spaans,
unpubl. data). The arrival of waders at Cape Cod, Massachusetts, in May from southeastern directions (Drury and Keith 1962, Nisbet 1963) also points to some transoceanic flights in spring.

Most other species, however, possibly take their spring migration route mainly across the South American continent by-passing the Guianas. Such a route is not unimaginable since many waders follow a route through the West Indies and the Mississippi Valley (Cooke 1912).

The reason for the differences in spring migration routes may lie with the geographical areas where the birds breed: a transoceanic flight for birds breeding in the most eastern parts of North America, and a route through the Caribbean and the Mississippi Valley for birds breeding in more western areas.

SUMMARY

During 1970-73, regular counts of North American waders were made along the Surinam coast to obtain quantitative data on their status and numerical fluctuations through the year. An extrapolation of these counts for the entire coast renders it likely that maximum numbers for the Lesser Yellowlegs, Short-billed Dowitcher, and the Semipalmated Sandpiper may amount to over 100,000, for the Greater Yellowlegs, Least Sandpiper, and possibly the Willet to 50–100,000, for the Semipalmated Plover, Spotted Sandpiper, Ruddy Turnstone, White-rumped Sandpiper, and the Stilt Sandpiper to 10–50,000. All other species, except the Black-bellied Plover and the Solitary Sandpiper, whose numbers may possibly amount to over 10,000, are less numerous.

Comparison of the data with counts from northeastern Venezuela suggests that in the fall many species reach the coast of Surinam through a non-stop flight across the Atlantic Ocean. In spring, many waders that spent the winter south of the Guianas seem to migrate across the South American continent by-passing the Guianas. Only the Short-billed Dowitcher, the Red Knot, and possibly the Greater Yellowlegs and the Willet, mainly fly directly to the Guianas and from there non-stop across the Atlantic Ocean to North America.

ACKNOWLEDGMENTS

My thanks are due to Dr. J. P. Schulz, Surinam Forest Service, who has called attention to the need for ornithological research along the Surinam coast, to Professor M. F. Mörzer Bruijns, Department of Nature Conservation, Agricultural University, Wageningen, and Professor K. H. Voous, Free University, Amsterdam, for supervision of the study. The study was financed by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO). The Surinam Forest Service provided boats and manpower to make possible the counts near Krofajapasi and surroundings, and to survey other rather inaccessible parts of the coast. My thanks are due to Mr. W. J. N. M. Verholt for drawing the figures, to Mr. H. A. Reichart for correcting the English text, and to Dr. D. G. Ainley and Dr. R. McNeil for their critical review of the manuscript. This paper was written while I held a temporary appointment at the Institute for Ecological Research, Arnhem, The Netherlands.

LITERATURE CITED


FEEDING OF NESTLING AND FLEDGLING
EASTERN BLUEBIRDS

Benedict C. Pinkowski

Several workers (Forbes 1903, Beal 1915, Cottam and Knappen 1939, Davison 1962) have described the prey consumed by adult Eastern Bluebirds (Sialia sialis). No definitive studies, however, have been done on the diet of nestling and fledgling bluebirds. In this paper I summarize the behavior of Eastern Bluebirds feeding young, describe the diet of nestling and fledgling bluebirds, and discuss the relationship between the foraging tactics of bluebirds (Goldman 1975, Pinkowski 1977) and types of prey fed to the young.

METHODS

Observations were made of Eastern Bluebirds nesting in nest boxes in Macomb Co., Michigan from 1971 to 1973. Nest sites were located in old fields adjacent to oak (Quercus sp.) woodlands. Details of the study area are published elsewhere (Pinkowski 1975, 1976a). Relevant aspects of bluebird foraging were dealt with in a companion paper (Pinkowski 1977).

I sampled 2503 nestling foods at 45 nests in 20 different nest sites and 275 fledgling foods for 12 different broods. Animal foods were grouped into 23 taxonomic categories (often families, occasionally orders or genera). I note individual prey species if these appeared important and follow Cantrall (1968) and Kaston (1948) in assigning names of various Orthopterans and spiders, respectively.

Nestling diet was sampled in part by using throat collars made from pipe-cleaners or heavy thread to prevent the young from swallowing food. The collars did not appear to harm the nestlings. Nests being sampled were checked every 20 to 30 min and young were not deprived of food for more than 1.5 to 2.5 h per day. Rarely was the same nest sampled on 2 consecutive days. Throat collars were difficult to use on small, recently-hatched young unless an assistant held the bird while a collar was being applied.

The use of throat collars may generate results biased in favor of large items because smaller items are likely to slip past the neck band (Ortians 1966). To offset this bias and enlarge the sample, I used 2 other methods of sampling foods: observations with a spotting scope (15-60×) and salvaging specimens (or portions thereof) from the nest cavity or from the crops of dead nestlings. Salvaged specimens included food dropped by the adults on trips to the nest and yielded small food items not likely to be obtained by other methods. I found observing nests with a spotting scope useful on older nestlings that could not be disturbed because of the possibility of premature fledging. This technique also permitted me to obtain a sample of 1359 foods fed by adults of known sex (bluebirds are sexually dichromatic), and it was the only procedure used to sample the food of fledglings. My presence 10-20 m from the nest did not disturb adult birds feeding nestlings or fledglings. Altogether, 54.3% of the nestling food data was obtained by using a spotting scope, 36.9% by using throat collars, and 8.8% by salvaging specimens.

I sampled foods evenly throughout the day and nestling period to make the data as representative of the diet as possible. Observations were conducted randomly to limit interactions among variables. For example, nestlings of a given age were observed at
different times of day to minimize the effects of diurnal variations in diet and feeding rate.

Food items fed to the young are summarized as the percent occurrence of the various taxonomic groups. Diurnal variation in prey and feeding rate was studied by assigning activities to 1 of 4 time periods: early morning (06:00–10:00 EST), late morning (10:00–13:00), afternoon (13:00–16:00), and early evening (16:00–20:00); 28.9%, 32.3%, 20.7%, and 18.1% of the nestling diet was sampled during the 4 time periods, respectively. Food sampling activity was proportionate to the number of active nests and extended from 9 May to 15 August. Young of most first (spring) broods hatch in mid-May and fledge in early June; second (summer) broods fledge between mid-July and mid-August (Pinkowski 1976b). Nestling food samples were obtained on a monthly basis as follows: May, 41.5%; June, 22.5%; July, 25.8%; and August, 10.3%. Sampling was done under all types of weather conditions, but results are slightly biased in favor of insects fed during non-rainy conditions.

Vegetable matter is sporadic in the diet of nestlings and plant specimens found in the nest cavity were not necessarily fed to the young because the brooding parent may regurgitate fruit seeds and skins (pers. obs.). For these reasons I analyzed the plant and animal portions of the nestling diet separately. I included fruit in tabulations of the fledgling diet because the limitations do not apply to young out of the nest.

Distances that adults foraged from the nest were recorded at 2 nests containing 3 and 5 young during the final week of the nestling period. Markers were placed in several directions at known intervals from the nest. Foraging bluebirds travel great distances and at least 2 (often 3) observers communicating by radio were required to follow the birds and determine distances and directions at which prey was obtained relative to the nest. Directions were placed in 1 of 16 categories (N, NNW, NW, etc.) for analysis of directional overlap by foraging adults.

Feeding rates are expressed in feedings per young per 15 h (= 1 day) and represent the average of results obtained for individual observation periods lasting 1–2 h (x = 86.5 min). I considered 1 trip to the nest with food as a single feeding regardless of the number or size of the prey. The male bluebird, like males of some other passerines, may offer food to the brooding female who in turn delivers it to the young. At some nests 70–90% of the nestlings’ food on the day of hatching is fed to them in this way. I considered food transfers, which become less common during the first week and are rare thereafter, as male feedings although the food is actually fed to the young by the female.

Frequency data, including the number of feedings of the male relative to the female, were examined for significant differences by Chi-square. Differences in absolute feeding rates (feedings/young/day) were tested by a one-way analysis of variance and Duncan’s multiple range test (Steel and Torrie 1960:107). Diversity indices for prey taxa (H = Σi pij log pij, where pij is the proportion of prey in the ith taxon) were calculated from information theory (Shannon and Weaver 1949). Because the diversity index is sensitive to sample size (Orians 1966, Pielou 1966) which in turn affects the number of prey categories, I use this index only to compare groups having similar sample sizes.

RESULTS AND DISCUSSION

Rate of feeding nestlings.—Female bluebirds offered proportionately more feedings to nestlings (54.8%) than males (45.2%). The difference is significant (χ2 = 19.0, P < 0.01, N = 2063 feedings), but considerable variation existed from one nest to another.
Feeding rate of both males and females did not depend on brood size. Males averaged 6.4, 4.8, and 5.5 feedings h to nests containing 3, 4, and 5 young, respectively. Corresponding figures for females are 6.5, 6.5, and 6.4 feedings/h. Consequently, young in nests containing 5 young received fewer feedings/day (35.5) than those in nests containing 4 young (42.2) or 3 young (64.3). That feeding rate did not increase with brood size may in part reflect a reduction in heat loss because of more insulation and less surface exposure in larger broods (Mertens 1969).

Bluebirds increased the feeding rate with nestling age during the first 17 days of the nestling period (Fig. 1). During the first few days after hatching there was an increase in prey size, and late in the nestling period adults occasionally brought more than one item per trip to the nest. These changes tended to offset the increase in feeding rate with nestling age.

The male and female contributed nearly equal proportions of the nestlings' food during the first 5 days of the nestling period (Fig. 1). Thereafter, the

![Graph](image-url)
Table 1

**Diurnal Variation in Feeding Rate of Eastern Bluebirds in Southeastern Michigan, 1971–1973**

<table>
<thead>
<tr>
<th></th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early Morning</td>
<td>224 (37.6%)</td>
<td>371 (62.4%)</td>
</tr>
<tr>
<td>Late Morning</td>
<td>281 (46.2%)</td>
<td>327 (53.8%)</td>
</tr>
<tr>
<td>Afternoon</td>
<td>202 (47.1%)</td>
<td>227 (52.9%)</td>
</tr>
<tr>
<td>Early Evening</td>
<td>225 (52.2%)</td>
<td>206 (47.8%)</td>
</tr>
</tbody>
</table>

Female ceased brooding during the day (Pinkowski 1975) and continued to increase her feeding rate until day 16; after day 16 the female feeding rate remained relatively constant (35.2–41.8 feedings/young/day; \( \bar{x} = 38.5 \)). The male feeding rate (feedings/young/day) was low on days 1–5 (\( \bar{x} = 13.0 \)), was significantly greater (\( \bar{x} = 24.8, P < 0.001 \)) and fairly constant (range = 17.6–28.8) on days 6–17, and significantly decreased (\( \bar{x} = 14.9; P < 0.01 \)) on days 18–21. Thus the overall increase in the feeding rate was at first attributable to an increase in the feeding rate of both adults and later was due to an increased rate by the female only. The decrease in the feeding rate late in the nestling period was largely attributable to a reduction in feeding by the male.

Some male bluebirds ceased feeding the young soon after fledging. On 3 occasions males began new nests with different mates before young of the previous nest were independent, a behavior not observed among females. In such instances the female continued to feed the brood and supplied all of its nutritional requirements.

Feeding rate (feedings/young/day) of males and females combined was greatest in early morning (49.2), lowest in the afternoon (39.9), and nearly identical in late morning and early evening (45.3 and 45.8, respectively). Although none of the differences in feeding rates for the 4 time periods is significant (\( P > 0.5 \)), proportionately more feedings observed in the early morning period (Table 1) were made by the female (\( \chi^2 = 35.8, P < 0.001 \)). Also, males fed more and females fed less during the successive time periods: the trend was significant (\( Z = 4.6, P < 0.001 \); Snedecor and Cochran 1967: 246). Thus there was a division of the daily “work load” by males and females that may function to keep the number of feedings to the young relatively constant throughout the day.

**FOOD FED TO NESTLINGS**

*Summary of invertebrate prey.*—Lepidopterous larvae comprised the largest percentage (32.4%) of animal food noted in the nestling diet and consisted of
several families, including Noctuidae ("cutworms"), Arctiidae, Pieridae, Geometridae, Notodontidae, Pyralidae, and Sphingidae. Adult Lepidoptera accounted for 3.6% of all animal foods recorded and consisted entirely of moths (Heterocera).

Orthopterans were the second largest group represented (25.6%), and included grasshoppers (Acrididae and one Tettigidae), 12.8%; crickets (Gryllidae, mostly the spring field cricket, Gryllus veletis; Alexander and Bigelow 1960), 9.3%; shield-bearing katydids (Tettigoniidae: Decticinae; Atlanticus testaceus), 1.6%; various other katydids (Tettigoniidae exclusive of Decticinae) such as Neoconcephalus sp., Amblycorypha sp., and Pterophylla sp., 1.5%; and mantids (Mantidae, all nymphs), 0.4%. Spiders (Arachnida: Araneae, including egg sacs, and a few Phalangida) were the third largest group (11.3%), and generally consisted of wandering, ground-dwelling species such as Lycosa frondicola.

Other taxa less frequent in the nestling diet were beetles (Coleoptera: mostly Phyllophaga sp., Melanotus sp., Scarites sp., and Cicindela sp. adults, and Carabidae and Elateridae larvae), 11.0%; earthworms (Annelida: Oligochaeta: Lumbricus sp.), 5.2%; various Hymenoptera (mostly carpenter ants, Camponotus sp., and some Ichneumonidae), 3.9%; and millipedes (Diplopoda), 2.3%.

Food items uncommon in the nestling diet were: leafhoppers (Homoptera: Cercopidae and Cicadellidae), 1.5%; sowbugs (Isopoda), 0.8%; snails and snail shells (Pulmonata), 1.2%; flies (Diptera), 0.5%; scorpion-flies (Mecoptera), 0.3%; dragonflies (Odonata: Anisoptera), 0.1%; Cicada, 0.1%; large bugs (Hemiptera), 0.1%; and lacewings (Neuroptera: Chrysopida), 0.04%. Unusual prey were 2 centipedes (Chilopoda, 0.1%) and 1 fairy shrimp (Anostraca, 0.04%).

Variations attributable to nestling age.—Spiders and Lepidoptera larvae were the primary food of recent hatchlings (Table 2). As the young mature more Orthoptera (Gryllidae and Acrididae), Coleoptera, and earthworms were fed. Prey diversity was lower early in the nestling period (H = 1.60 for young 1–5 days old) than later (H = 2.05 and 2.04 for young 6–10 and 11–18 days old, respectively).

Nine of 12 food items fed to young 1 day old or less were spiders. Twelve spider species were noted only once during the sampling period; 9 of these species occurred only in the diet of nestlings 4 days old or less. Other passerines also exhibit a preference to feed spiders to recent hatchlings (Royama 1970). Small nestlings must be fed small, easily digested foods, and prey with a high energy content relative to its size would seem most desirable. Spiders have a soft abdomen, lack coarse appendages, and have greater caloric
Table 2


<table>
<thead>
<tr>
<th></th>
<th>0–5 Days Old</th>
<th>6–10 Days Old</th>
<th>11–18 Days Old</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No.</td>
<td>%</td>
<td>No.</td>
</tr>
<tr>
<td>Lepidoptera larvae</td>
<td>163</td>
<td>41.6</td>
<td>192</td>
</tr>
<tr>
<td>Arachnida</td>
<td>121</td>
<td>30.9</td>
<td>63</td>
</tr>
<tr>
<td>Acridida</td>
<td>27</td>
<td>6.9</td>
<td>86</td>
</tr>
<tr>
<td>Gryllida</td>
<td>29</td>
<td>7.4</td>
<td>56</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>4</td>
<td>1.0</td>
<td>28</td>
</tr>
<tr>
<td>Heterocera</td>
<td>26</td>
<td>6.6</td>
<td>33</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>4</td>
<td>1.0</td>
<td>40</td>
</tr>
<tr>
<td>Lumbricus sp.</td>
<td>4</td>
<td>1.0</td>
<td>12</td>
</tr>
<tr>
<td>Atlanticus testaceus</td>
<td>3</td>
<td>0.8</td>
<td>13</td>
</tr>
<tr>
<td>Tettigonidae</td>
<td>2</td>
<td>0.5</td>
<td>3</td>
</tr>
</tbody>
</table>

equivalents than Acridids and earthworms (cal/g dry wt; Golley 1961, Van Hook 1971) that bluebirds feed more often to older nestlings.

Large spiders (e.g., *Lycosa frondicola* and *Schizocosa avida*) were noted in the diet of older nestlings, and male and female spiders of dimorphic species were selected by size for young of different ages. Eleven *L. frondicola* males were fed to nestlings averaging 5.3 days old, whereas 7 females of this species (which are larger than males) were fed to young an average of 7.1 days old. A similar trend appears among some Orthoptera; nymphs of the grasshopper *Melanoplus bivittatus* were fed to 3-day-old nestlings and the coarser adults were not fed until day 7 (males, which are smaller than females) and day 9 (females).

**Variations attributable to season.**—Invertebrate prey fed to nestlings and tabulated on a monthly basis revealed that spiders were fed more in May and June (13.1% and 14.3%, respectively) than July (7.9%) and August (4.4%). The seasonal decline in frequency of spiders was not entirely attributable to a decrease in availability. *L. frondicola* and *Phidippus princeps*, the most common spiders in the nestling diet in spring, were not fed after early June (Fig. 2) although both species are present from April to October at the latitude of my study area (Dondale 1971).

Ground-dwelling spiders belonging to the family Lycosidae (e.g., *L. frondicola*, *Trochosa terricola*) were more common in the diet of nestlings in spring. In summer, however, spiders of the family Thomisidae (e.g., *Tibellus oblongus*, *Xysticus elegans*) that dwell on herbaceous plants and tree trunks (Lowrie 1948) were more common. The Lycosid *Schizocosa avida*
is common in summer but this species, like the Thomisids and unlike the other Lycosids, is phytophilous (Kuenzler 1958).

Lepidoptera adults (all moths) were more common in the nestling diet in summer (5.6%) than in spring (2.9%). Earthworms and Coleoptera were staple food items in spring, especially during rainy periods, but became less important later in the season. Earthworms comprised 10.8% of the nestling diet in May and 3.3% in June, but were absent after 1 July. Coleoptera comprised 17.9% of the diet in May, 8.3% in June, 5.9% in July, and 0.8% in August. Hymenoptera were more common in May (4.7%) and June (4.8%), when swarming carpenter ants were frequently taken, and less common in July (2.6%) and August (2.4%).

Lepidoptera larvae were more common in the diet during May (35.4%) and June (41.8%) than July (20.3%) and August (28.9%). As was the case for spiders, seasonal changes in occurrence of larval Lepidoptera reflected changes in availability, but geophilous forms were more common early in the season. Cutworms (Noctuidae larvae) accounted for 46.6% (N = 393) of all Lepidoptera larvae noted in the diet. One species, the bronzed cutworm (*Nepheleodes minians*), comprised 48.6% of the cutworms recorded and is typical of the prey belonging to this taxon in that it feeds at night but is found on the ground during the day. The percentage of cutworms among all Lepidoptera larvae fed to nestlings was greatest in May (74.6%, N = 134) and decreased in June (36.4%, N = 140), July (33.7%, N = 83), and August
Fig. 3. Seasonal variation of Orthoptera taxa in the diet of nestling bluebirds. Numerals indicate sample sizes. All taxa noted at least 3 times are included. The solid portion of the time scale indicates the sampling period. Individual species and genera are represented as follows: Gryllus sp. (G), Pardalophora apiculata (Pa), Arphia sulphurea (As), Chortophaga viridifasciata (Cv), Melanoplus viridipes (Mv), Atlanticus testaceus (At), Pseudopomala brachyptera (Pb), Melanoplus sanguinipes (Ms), Melanoplus bivittatus (Mb), Melanoplus confusus (Mc), Chorthippus curtipennis (Cc), Dissosteira carolina (Dc), Neoconocephalus sp. (N), and Mantis sp. (M).

(11.4%, N = 35). Larvae of other Lepidoptera families (e.g., Geometridae) that inhabit trees and vegetation became increasingly common as the season progressed, but maximum consumption of all families combined occurred in June.

Orthoptera were more common in the diet in summer than spring, although individual species recorded were dependent on season (Fig. 3). Gryllus veletis, the most common Orthoptera noted, increased steadily from May through July (5.1%, 8.4%, and 17.6% for the 3 months, respectively). G. veletis nymphs were fed in mid-May, adults in late May, and peak predation occurred in mid-July. Acrididae increased steadily from May to August (5.5%, 9.2%, 23.4%, and 26.9% for each month, respectively).
The incidence of various Orthoptera in the nestling diet differed little from the chronological appearance of the various species in the study area (pers. obs.; Cantrall 1968). Orthopteran species of similar size and habits, however, complemented each other in the diet on a seasonal basis. In summer adults of *Atlanticus testaceus*, a large, geophilous species, replaced *G. veletis* in the diet. Large vernal Acridids that overwinter as nymphs in southern Michigan (*Chortiphaga viridifasciata* and *Pardalophora apiculata*) were replaced in summer by other large Acridids (*Dissosteira carolina, Melanoplus bivittatus*). Similarly, the smaller Acridids *Arphia sulphurea* and *Melanoplus viridipes* were common in spring and were replaced in summer by *Pseudopomala brachyptera, Chorthippus curtipennis, Melanoplus confusus*, and *M. sanguinipes*, which are also small.

Phytophilous Orthoptera (*Neoconocephalus* sp. and *Mantis* sp.) were fed to nestlings only in summer. Thus for all 3 of the major prey groups (*Lepidoptera* larvae, *Arachnids*, and Orthoptera), bluebirds tended to select geophilous species in spring and phytophilous species in summer. Phytophilous invertebrates were undoubtedly more abundant relative to geophilous taxa late in the season as vegetation height increased, but in some cases geophilous prey were present late in the season, but were ignored by bluebirds.

Evans (1964) found that Vesper Sparrows (*Poecetes gramineus*), Song Sparrows (*Melospiza melodia*), and Chipping Sparrows (*Spizella passerina*) breeding in southern Michigan use a greater variety of food in summer than spring. I found this somewhat true of bluebirds: 19 of the 23 (82.6%) prey categories were represented during July whereas only 14 (60.9%) were recorded in May. Diversity indices were higher in July (2.24) and August (2.09) than in May (1.95) and June (1.96).

*Variations attributable to time of day.*—Several classes of prey, including *Arachnida*, *Coleoptera*, *Heterocera*, and *Tettigoniidae*, displayed no frequency variation with time of day; others, however, were more variable. *Gryllidae* were fed more in early morning (13.7%) and early evening (13.5%) than late morning (4.9%) and afternoon (4.2%). *Acrididae* displayed the reverse pattern (19.0% in the afternoon, 18.7% in the late morning, 12.8% in early evening, and 8.0% in early morning). Thus both *Gryllidae* and *Acrididae* were apparently preyed upon most often when they were most active.

*Lepidoptera* larvae were abundant (39.2–44.7%) from early morning until late afternoon and less common (29.2%) in early evening. *Hymenoptera* were most abundant in early evening (8.3%) when bluebirds frequently engage in flycatching (Pinkowski 1977); they were least common in the afternoon (0.6%) and intermediate (4–5%) in the other periods. *Earthworms* were most common in early evening (8.7%) and afternoon (7.3%), and less common (1.6–3.0%) in other periods.
Prey diversity was greatest in early evening (H = 2.18), partly because aerial insects (Hymenoptera, Diptera) were added to the diet at that time. Diversity was lowest in the afternoon (H = 1.72) when feeding rate was reduced, and was greater in late morning (H = 1.93) and early morning (H = 1.90).

Small stones, snails, and snail shells function as grit (Royama 1970) and were noted only in the early morning. The female bluebird apparently supplies nearly all of the grit required by nestlings. Seven observed feedings of grit were all made by the female.

Variations attributable to weather.—Precipitation (mostly rainfall except during March) increased during the 3 years of study; 15.3 cm of precipitation fell from 1 March to 30 June 1971, and 25.6 cm and 38.6 cm were recorded for the same period in 1972 and 1973, respectively. Annual incidence of Acrididae in the diet decreased with the increasing precipitation (20.1%, 16.1%, and 4.7% for the 3 consecutive years): the same trend occurred among Gryllidae (17.1%, 8.5%, and 4.9%). Some Orthoptera, especially grasshoppers, flourish during periods of drought and are reduced in numbers during rainy years (Shelford 1963:318, Scharff 1954).

More earthworms were taken in 1973 (14.0%) than in 1971 (2.9%) and 1972 (1.5%). A paucity of Lepidoptera larvae in the diet in 1971 (19.9%) compared with 1973 (35.7%) and 1972 (38.2%) may have been attributable to death of these insects from desiccation during dry conditions (Andrewartha and Birch 1960) or other factors such as lack of food. In any event, bluebirds tend to feed Orthoptera during dry seasons and Lepidoptera larvae and earthworms during rainy seasons, presumably because of differences in relative availability.

Fruit fed to nestlings.—Vegetable matter, uncommon in the diet of nestlings, was noted at only 4 of 45 nests observed. The fruits involved were mulberries (Morus sp.), raspberries (Rubus sp.), dogwood (Cornus stolonifera), cherry (Prunus virginiana), and honeysuckle (Lonicera sp.). Fruit was not fed before late June, when it became abundant in the study area. At 2 of the 4 nests, each containing nestlings within a few days of fledging, fruit comprised 33.0% and 37.0% of the nestling diet over 3 and 5 day periods, respectively (approximately 15 h observation in each case). At the 2 other nests fruit was noted only once; each instance involved older nestlings (≥14 days old).

Morton (1973) concluded that a fruit diet prolongs nestling development and is selected against as a food for poikilothermic young on account of its low protein content. The altricial strategy, he argues, requires that the small young be able to use food principally for growth and not for heat production (because the nestlings' heat requirements are satisfied by brooding). Fruit, therefore, is not a dietary constituent of young bluebirds until the last week of
the nestling period, when the nestlings are completely endothermic (Pinkowski 1975).

Partitioning of the feeding niche.—A foraging pair of adult birds may reduce competition by differentially using the feeding resources available to them without necessarily involving secondary sexual dimorphism (Ligon 1968, Jackson 1970). I noted no difference in the diversity of foods fed to the young by male \( H = 1.89 \) and female \( H = 1.87 \) bluebirds. Males, however, fed significantly more Gryllidae \( x^2 = 4.9, P < 0.05 \) and earthworms \( x^2 = 21.9, P < 0.001 \) than females; females fed more Acrididae \( x^2 = 5.4, P < 0.05 \), Hymenoptera \( x^2 = 4.2, P < 0.05 \), and Arachnida \( x^2 = 4.9, P < 0.05 \) than males. Little difference was noted among other prey categories including moths \( x^2 = 0.8, P > 0.3 \) and Lepidoptera larvae \( P > 0.9 \).

I could not attribute differences in foods fed by males and females to different feeding rates of males and females relative to age of the nestlings. Earthworms and crickets, preferred foods of males, were most common in the diet of older nestlings that were fed more by females. Spiders were relatively uncommon late in the nestling period when females fed more often than males. Although grasshoppers were common in the diet of older nestlings, Pinkowski (1974) noted that captive female Eastern Bluebirds and Mountain Bluebirds \( (Sialia currucoides) \) preferred to feed grasshoppers to nestlings.

Differential prey use may result from differential use of the feeding range by males and females. Using pooled data for 2 nests, I found that male bluebirds obtained prey for nestlings closer to the nest site \( \bar{x} = 113.6 \) m, \( SD = 99.4, N = 256 \) than females \( \bar{x} = 152.4 \) m, \( SD = 117.3, N = 182; t = 3.7, P < 0.01 \). Indices of overlap (Horn 1966) for directions that males and females obtained prey were great \( (0.875 \) and \( 0.902) \); apparently food resources were not partitioned on a directional basis.

In some areas male and female bluebirds forage at equal distances from the nest (Pinkowski 1974, Goldman 1975). When there is a difference in foraging distances, however, evidently the male remains closer to the nest, possibly because male bluebirds play a greater role than females in defence of the nest cavity against conspecific intruders. Females of some open-nesting species such as the Bobolink \( (Dolichonyx oryzivorus) \) and Henslow’s Sparrow \( (Ammodramus henslowii) \) forage closer to the nest than males (Wiens 1969, Robins 1971).

Power (1974:88–99) related foraging distance of adults to brood size (work load) in the Mountain Bluebird. For the 2 Eastern Bluebird nests I examined, however, the adults with 3 young foraged farther from the nest \( \bar{x} = 166.2 \) m than adults with 5 young \( \bar{x} = 96.2 \) m; \( t = 7.1, P < 0.001 \). Eastern Bluebirds are more dependent on feeding perches than Mountain Bluebirds and are
known to vary foraging range according to perch distribution (Pinkowski 1974, 1977). Thus habitat quality appears more important than the number of young in the nest in determining how far adults travel in search of food.

FEEDING OF FLEDGLINGS

Foods fed to fledglings differ from those fed to nestlings. Lepidopterous larvae were more common in the fledgling diet (44.0% of all fledgling foods recorded), reflecting peak consumption in June when most fledglings were out of the nest. Earthworms (11.4%) and Coleoptera (7.7%) were more common in the fledgling diet than the nestling diet, but the reverse was true for Acrididae (8.8%), Arachnida (4.4%), Gryllidae (3.3%), and Heterocera (3.3%). Fruit (mulberries and cherries) comprised 11.0% of the fledgling diet, but was noted only during the summer period (July and August). General observations indicated that the adults feed smaller items to fledglings than nestlings.

Feeding patterns of adults foraging for fledglings differ from those of adults feeding nestlings. Fledgling bluebirds spend most of their time in large trees and alternate active and inactive periods; they begin calling when hungry and, depending on food availability, receive several feedings until satiated. Adults obtain many food items within a few meters of the fledglings, often by gleaning from the tree tops, and many small items may be fed in rapid succession to young out of the nest. This is in contrast to the long trips with large items made regularly by adults with young in the nest.

CONCLUSIONS

Prey availability is important in determining dietary constituents of young bluebirds. Weather and time of day influence prey activity and abundance and hence affect what is fed to the young. The presence of smaller nestlings somewhat restricts prey selection because older young are fed a greater variety of foods. As the spectrum of suitable prey increases with nestling age, however, so does the amount of food required by the young and consequently the feeding rate of adults. These changes would tend to equalize the time and energy expended by adults during the duration of the nestling period.

The data obtained in this study corroborate Goldman’s (1975) conclusion that bluebirds feed large food items to nestlings. Lepidoptera larvae (especially cutworms) are the preferred food for nestlings. Beal (1915), however, states that Orthoptera are preferred by adult bluebirds and noted that Coleoptera are nearly twice as common in the diet of adults (29.9%) as I found in the diet of nestlings. Although Orthoptera and Coleoptera are large, their relative infrequency in the diet of the young may be explained by their coarseness.
Coarse foods require more preparation and thereby reduce caloric yield per unit time, the basic determinant of food value (Emlen 1966).

Foraging bluebirds locate prey from a distance by using conspicuous feeding perches: in spring most prey is obtained after a short "drop" to the ground, but in summer there is an increased use of tactics such as gleaning and flycatching that result in prey capture above ground (Pinkowski 1977). Analysis of seasonal variation in prey taxa suggests that the seasonal trend in foraging tactics is independently related to both a seasonal increase in vegetation biomass (height and density) and an increase in the abundance of invertebrates living above ground. Bluebirds rarely feed by dropping onto the ground in areas having tall, dense vegetation, probably because doing so would often require them to relocate prey from close range and not from a conspicuous and elevated position (Pinkowski 1974:66). Thus late in the season bluebirds do not feed upon some geophilous prey taxa (earthworms, cutworms, Coleoptera, and some spiders) that are still available, but instead exploit phytophilous and aerial prey (moths and certain spiders, Lepidoptera larvae, and Orthoptera) that are more abundant and conspicuous from a distance than geophilous prey. By changing their predatory tactics on a seasonal basis, bluebirds are able to exploit changes in prey availability as well as maintain the optimum predatory efficiency permitted by their perch-feeding habit.

SUMMARY

The behavior of adult Eastern Bluebirds feeding nestlings and fledglings and the diet of young bluebirds were studied in southeastern Michigan from 1971 to 1973. Females fed nestlings more often than males. The feeding frequency increased with nestling age until just prior to fledging, when a decline occurred. Feeding rate of males and females combined was relatively constant throughout the day although females fed young more often earlier in the day and male feeding rate was greater later in the day.

Lepidoptera larvae were the most common food of both nestlings and fledglings and comprised 32.4% of the nestling diet. Orthoptera (mostly Acrididae and Gryllidae) were also common (25.6%), especially in summer. Spiders (11.3%) were particularly important early in the season and for newly-hatched young. Fruit was uncommon in the diet of nestlings but was fed to fledglings in summer and made up 11.0% of all fledgling foods recorded.

Adult males and females fed different foods to the young, thereby partitioning the feeding niche. Males fed significantly larger percentages of Gryllidae and earthworms; females fed larger percentages of Arachnida and Acrididae.

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245 COUNTY LINE ROAD, BRIDGEVILLE, PA 15017. ACCEPTED 11 NOV. 1976.
DIFFERENTIAL USE OF FRESH WATER ENVIRONMENTS BY WINTERING WATERFOWL OF COASTAL TEXAS

DONALD H. WHITE AND DOUGLAS JAMES

Species having similar life styles (Ralph 1975) characteristically occupy different ecological niches (Hutchinson 1957, 1965) within shared environments. Many workers have shown that this principle seems to be operative in avian communities (MacArthur 1958, Cody 1968, James 1971, Posey 1974, Whitmore 1975). Our study was conducted to determine how feeding flocks of wintering waterfowl coexisted in feeding site selection, what environmental factors that were measured were the most important in certain aspects of niche separation, and how the niches were arranged in the aquatic community at the study site.

METHODS AND MATERIALS

Study area.—Data were collected from early October through late December 1973 from 2 adjacent ox-bow lakes on the grounds of the Welder Wildlife Foundation in San Patricio County near Sinton, Texas. These fresh water lakes were up to 2.5 m deep but averaged about 1.5 m in the middle. A broad zone of semi-aquatic grasses (Paspalum and Panicum) occupied the perimeters and burhead (Echinodorus rostratus), southern cut-grass (Leersia hexandra), and bulrush (Scirpus californicus) occurred in isolated small patches. The transition zone from emergent semi-aquatic vegetation sometimes occurred over 90 m from shore, but was quite variable in position. Extensive floating or partly submerged patches of aquatic vegetation were dominated by southern naiad (Najas guadalupensis), star grass (Heteranthera liebmannii), musk grass (Chara), and duck weed (Lemma perpusilla).

Large numbers of waterfowl use the coastal region of southern Texas during the fall and winter months (Bellrose 1976) therefore, references to “wintering waterfowl” and “wintering grounds” throughout this paper are made on this basis. Most of the individuals of some species such as the Fulvous Whistling Duck and Blue-winged Teal have moved further south by late December or early January (Bennett 1938, Bellrose 1976) and may not be considered as truly wintering species of southern Texas. Nevertheless, these 2 species were included as they were present when the study was conducted.

Field methods.—The species studied were: Mottled Duck (Anas fulvigula), Pintail (Anas acuta), Gadwall (Anas strepera), American Wigeon (Anas americana), Northern Shoveler (Anas clypeata), Blue-winged Teal (Anas discors), Green-winged Teal (Anas crecca), Fulvous Whistling Duck (Dendrocygna bicolor), Redhead (Aythya americana), Canvasback (Aythya valisineria), Ring-necked Duck (Aythya collaris), Lesser Scaup (Aythya affinis), Ruddy Duck (Oxyura jamaicensis), and American Coot (Fulica americana).

To characterize the environments of feeding waterfowl flocks 20 factors were measured in the field comprising social, vegetational, physical, and chemical properties. Social factors included: total number of ducks in flock, number of species in flock, number in flock of species being sampled, number feeding of species being sampled, number of
cots present in flock, and distance to neighboring flock (m). *Vegetational factors were:* % emergent vegetation, emergent vegetation height (cm), and % floating and/or submerged vegetation. *Physical factors were:* depth of water at feeding site (cm), distance of flock from shore (m), turbidity of water at feeding site (Jackson turbidity units), % cloud cover, and wind velocity (km/hr). *The chemical measurements of the water at feeding locations were:* pH, dissolved oxygen (ppm), total nitrogen (ppm), total phosphorous (ppm), total calcium (ppm), and conductivity (micromhos/cm).

Twenty-five samples of the 20 environmental factors were measured for each species. Feeding flocks were sampled at random and data collecting for each species was distributed as much as possible during the study period to eliminate time of sampling as a bias. Also, 60 random samples of the environmental factors (excluding social factors) were taken to determine the general nature of the habitat available in the aquatic environment at Welder. The random samples were selected by superimposing a grid on a map of the study area and using numbers from a random table as X and Y coordinates to designate approximate sample locations. Means and standard deviations of the factors measured in the study for each species and the random habitat samples are included in White (1975).

The feeding flocks of wintering waterfowl were studied regardless of size. Although loose mixed-species flocks often were encountered, the ducks tended to separate according to species. Therefore, the approximate center of each species flock within loose mixed flocks served as the sample point from which measurements were made. Sampling began at daylight and continued throughout the day. A canoe and hip boots were used in collecting data. Observations were made with binoculars and a telescope. Social factors were recorded from afar and the location of nearest neighboring flocks was noted before disturbing the ducks to measure other factors.

Flock-center locations were marked using a buoy and samples were taken within a radius of approximately 3 m from this point. Percentages of emergent vegetation and floating and or submerged vegetation were estimated by making 50 random observations within the sampling perimeter using a sighting tube (Winkworth and Goodall 1962) and doubling the total sightings having plants intersected by crosshairs.

Water depth was measured with a meterstick or weighted nylon cord; distances to shore and to nearest neighboring flock were measured with a range finder; wind velocity was measured with an anemometer held at eye level; cloud cover was estimated. A water sample was taken at each site and analyzed at the end of the day for turbidity and chemical factors using a Hach water analysis kit.

Population densities of the waterfowl species included in this study were highly variable. For example, Pintails generally were much more abundant than Mottled Ducks, Canvasbacks, or Ruddy Ducks. Total numbers of the various species using the lakes at Welder varied from day to day since waterfowl are highly mobile and may cover a wide range of habitats. Certainly it is possible that on one or several occasions measurements were taken on the same individuals of a particular species. This should not bias the data (James 1971) since individuals of a species generally are indicative of that species as a whole. Population estimates for the 3 month period are not available per se, however see White (1975) for mean flock sizes based on 25 observations for each species.

*Data analysis.*—The IBM-360 Model 50 digital computer at the University of Arkansas was used for all data analyses. Principal component (PC) analysis (Morrison 1967) based on correlations between untransformed data was used to determine the environmental factors that varied the most in niche relationships. After transforming the data to minimize heteroscedasticity and non-normality (Box and Cox 1964, Andrews et al. 1971), multivariate analysis of variance (Cooley and Lohnes 1971) with a step-down procedure
(Bargman 1962) was used to determine how the species were arranged with respect to the environmental factors that were important in separating species. The canonical scores from the preceding analysis were subjected to 1-way analysis of variance with Duncan's multiple range test (Steel and Torrie 1960) to determine the degree of species environmental overlap.

RESULTS

The following PC analyses were conducted on the combined species data. The first included all of the 20 environmental factors measured in the study; the second involved only the 14 non-social factors (vegetational, physical, and chemical). In both analyses the initial principal components identified the combination of factors that described the greatest variation in the data sets. This represented the breadths and limits of the ecological niches based on the factors that were measured. Niche differences were evaluated using multivariate analysis of variance and associated procedures.

Overall relationships.—The PC analysis that included all of the 20 environmental factors measured in the study gave an overall account of niche structure for the species, including the social environment as a niche component. The first principal component (PC-I) of the combined data set for all species showed high correlation values for 4 social factors (Table 1). This indicated that waterfowl as a group varied the most in social activity. The second principal component (PC-II) showed high correlation values for water depth at feeding site, vegetational percentages, calcium content, and conductivity. Combinations of these factors characterize specific feeding sites. Together PC-I and PC-II accounted for 30% of the total environmental variance.

A 2-dimensional representation of the distribution of the ecological niches (Fig. 1) was produced by plotting the mean PC-I and PC-II scores (James 1971). Relative niche widths are shown by 1% confidence ellipses circumscribing the mean of each species data set. The ellipses are very small indicators of niche width; larger ellipses would tend to mask relationships due to broad overlap. Social activity, based on those social factors with high correlation values in Table 1, increases from left to right along the PC-I axis (Fig. 1). Water depth at feeding site and floating and/or submerged vegetation increase from top to bottom along the PC-II axis, whereas calcium and conductivity (high values equated to high productivity; Oriens 1966, Russell-Hunter 1970) and emergent vegetation decrease in the same direction. Each species position within the total environmental space is determined by its individual responses to the definitive factors characterizing the space.

The Redhead and Canvasback were quite similar in response and exhibited the most social activity, whereas the Mottled Duck was the least social (Fig. 1). The Ruddy Duck and Gadwall generally occupied the deeper water with copious aquatic vegetation (Sincock 1963, Bellrose 1976) while at the other
<table>
<thead>
<tr>
<th>Environmental Factors</th>
<th>All Factors Combined Species Data</th>
<th>All Except Social Factors Combined Species Data</th>
<th>Random Samples</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PC-I</td>
<td>PC-II</td>
<td>PC-I</td>
</tr>
<tr>
<td><strong>Social</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Total number in flock</td>
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</tr>
<tr>
<td>2. Number of species in flock</td>
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<td></td>
</tr>
<tr>
<td>3. Number in flock of species being sampled</td>
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<td>.33</td>
<td></td>
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<tr>
<td>4. Number feeding of species being sampled</td>
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</tr>
<tr>
<td>5. Number of coots in flock</td>
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</tr>
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<td>6. Distance to nearest neighbor flock</td>
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<tr>
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<td>7. Percent emergent vegetation</td>
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<td>8. Emergent vegetation height</td>
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<td>9. Percent floating and/or submerged vegetation</td>
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<td>10. Depth of water at feeding site</td>
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<td>11. Distance to shore</td>
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<td><strong>Chemical</strong></td>
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<td>16. Dissolved oxygen</td>
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<td>20. Conductivity</td>
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extreme the Green-winged Teal and Mottled Duck favored shallow productive waters with much emergent vegetation (Singleton 1968, Bellrose 1976). Grouped ellipses show similarities in mean niche characteristics of various waterfowl such as the closeness in the Blue-winged Teal, Northern Shoveler, and Ring-necked Duck. The American Coot and Fulvous Whistling Duck had the largest niche sizes, the Ring-necked Duck and Ruddy Duck the smallest. The Redhead and Canvasback were more specialized in feeding site than in breadth of social behavior, tending to be more social in shallower water.

Habitat relationships.—The PC analysis of the 14 non-social factors depicted the habitat space occupied by the whole waterfowl community and delineated the realized habitat niches (Hutchinson 1957, 1965) exhibited by the various species within this space. The first principal component (PC-I) showed that water depth at feeding site, vegetational percentages, calcium, and conductivity were the factors contributing to the most variability for waterfowl as a group (Table 1); these were the same factors identified by PC-II in the preceding
INCREASING WATER DEPTH AND DEEP-WATER PLANTS

INCREASING SHALLOW-WATER PLANTS AND PRODUCTIVITY

Fig. 2. Waterfowl ordination with 1% confidence ellipses based on species values and means for scores of the first (abscissa) and second (ordinate) principal components; only vegetational, physical, and chemical environmental factors included in the analysis.

analysis and characterized feeding site habitats. Oxygen content and pH were highly correlated with the second principal component (PC-II) and pertained to the nature of trophic activity in the water (Table 1). High pH and water oxygen levels are associated with sites dominated by photosynthesis in submerged plants. Sites dominated by organic decay are relatively low in oxygen and pH.

Waterfowl habitat preferences are shown in Fig. 2 with 1% confidence ellipses representing relative niche sizes. The sequence of species from left to right on the abscissa (PC-I) is similar to the equivalent PC-II from top to bottom on the ordinate in Fig. 1 (the slight differences being due to the elimination of social factor effects for the principal components in Fig. 2). With respect to PC-II (Fig. 2) the Lesser Scaup occupied sites with the highest pH and oxygen levels, the Mottled Duck and Blue-winged Teal at the opposite extreme. Interesting relationships occurred such as the Green-winged Teal favoring more photosynthesis dominated sites in shallow water compared to the Mottled Duck, while the Blue-winged Teal preferred decay dominated sites in deeper water. The Canvasback and Redhead had the smallest niche sizes with respect to habitat axes, both teals the largest. The 2 principal components described 35% of the total habitat variance.

Comparison of PC correlations for the random habitat samples (Table 1) with those from separate analyses of each waterfowl species (for the latter PC
data consult White 1975) identified the species that responded directly to the existing habitat contrasted to those that made special habitat adjustments. The Mottled Duck, Green-winged Teal, Shoveler, American Wigeon, American Coot, Redhead, Canvasback, and Lesser Scaup exhibited moderate to high correlations for some or all of the factors that were highly correlated with PC-I for the random habitat samples (White 1975). Thus they responded directly to the range in habitat conditions that was available in the lakes studied. The other species, showing deviant PC correlations, selected special habitat conditions from the common conditions existing there. Even those that responded directly to the existing habitat were separated along the total habitat cline as was evidenced by the existence of different species means for habitat factors (White 1975). Principal components following PC-I differed progressively more among species, and between species and the random samples. This stressed the differing species specific habitat responses associated with the decreasing variance of the later PC's since essential requirements would tend to be constantly present and thus less variable.

Environmental differences.—Relative positions of waterfowl niches shown by PC analysis do not indicate whether species actually differ in responses, but employing multivariate analysis of variance showed that differences were significant ($\alpha = 0.05$). The latter analysis differs from PC analysis in computing new variables (canonical variables) which are linear functions of the original ones, but stressing those factors that effectively separate respective populations (Sokal and Rohlfl 1969). An associated step-down analysis indicated that water depth at feeding site and % emergent vegetation, both important factors in the first canonical variable, were statistically significant in separating species. Vegetation height also was highly correlated with the first canonical variable. Floating and/or submerged vegetation and calcium content were highly correlated with the second canonical variable and thus were important in characterizing the species environments, but were not statistically significant in separating the species.

By plotting means of the first and second canonical variables for each species (James 1971), an ordination showing maximum separation is obtained (Fig. 3). The species ordering follows an environmental cline from shallow water on the left to deep water on the right with associated decreasing % emergent vegetation from left to right.

To determine which of the species overlapped in their requirements, the first canonical variable scores for all samples of each species were subjected to a common one-way analysis of variance with Duncan's multiple range test. Four distinct groups were significantly separated ($\alpha = 0.05$) from all others and each group was associated with a particular segment of the aquatic community (Fig. 4). Overlap in niche requirements among species along the
INCREASING WATER DEPTH

DEEP-WATER PLANTS AND CALCIUM INCREASING

Fig. 3. Waterfowl ordination using means of the first and second canonical variables from multivariate analysis of variance, thus stressing factors that provide maximum separation among species.

cline is represented by the thin horizontal lines beneath the heavy ordination line.

Segment A (Fig. 4) represented very shallow water (1–30 cm) with abundant emergent vegetation near lake shorelines. The Mottled Duck occupied this part of the littoral zone and was never recorded elsewhere. Segment B contained 3 species (Blue-winged Teal, Green-winged Teal, and Northern Shoveler) and represented the part of the littoral zone having moderate amounts of semi-aquatic and aquatic vegetation with shallow to moderate water depths (30–88 cm). Segment C had abundant aquatic vegetation, sparse emergent vegetation, and moderate water depths (88–114 cm). Six species (Fulvous Whistling Duck, Pintail, Gadwall, American Wigeon, Ring-necked Duck, and American Coot) occupied this region mainly, but some overlap is seen between species in segments B and C. Thus the species in these subgroups were not as exclusive in requirements as was the shoreline restricted Mottled Duck. Segment D, representing open deep water (114–213 cm) with little emergent vegetation habitat was frequented by the Ruddy Duck, Redhead, Canvasback, and Lesser Scaup.

The general trend of the species ordering along a community transition is well illustrated in Fig. 5. The species arrangement on the abscissa is in the same order as in Figures 3 and 4, and the means for water depth at feeding site, % emergent vegetation, and % floating and/or submerged vegetation are plotted for each species (see White 1975 for tables giving mean values). The
distinctiveness of environmental preferences (Weller 1975) for each subgroup is evident. Notice that puddle ducks are found in shallow to moderate water depths (Weller 1975), diving ducks in deep water, and the 2 groups are at opposite ends of the cline. The most species, 9 in 2 subgroups (B and C), are rather closely packed in the middle of the sequence (Fig. 4) where water depths are moderate (88–114 cm) and truly aquatic vegetation is greatest (Fig. 5).

The pattern of waterfowl preferences vs. habitat availability is shown by plotting the PC scores obtained from analyzing only the 60 random samples and establishing a 95% confidence ellipse based on these samples (Fig. 6). This represents most of the available habitat space at the study area on the Welder Foundation grounds (social factors not included in random samples). Increasing water depth and distance to shore from left to right on the abscissa (Fig. 6) and amount of emergent vegetation increasing in the opposite direction were highly correlated with PC-I (Table 1). Aquatic vegetation decreasing upward on the ordinate was highly correlated with PC-II. Together PC-I and PC-II accounted for 41% of the total variance. Directional cosines from the random samples PC analysis were used as weights to generate corresponding PC scores for each species. The means of these scores for each species plotted in Fig. 6 show that the species were clumped near the center of the available habitat space.
DISCUSSION

Recent multivariate studies of birds in various habitat types indicate that species may be arranged horizontally as well as vertically in response to vegetational characteristics. Grassland birds were distributed vertically in the tall vegetation by differences in feeding height and horizontally by differences in habitat preferences (Cody 1968). Forest birds were distributed vertically and horizontally along a continuum from forest edge to mature forest (James 1971) and old-field birds were scattered along a cline in shrubbiness habitat (Posey 1974). Our findings show that waterfowl too were distributed along an environmental cline, but an aquatic one rather than terrestrial. Social characteristics proved diagnostic too.

Despite much overlap in groups of waterfowl species, each species occupied a definite position with respect to sets of environmental factors ranging from very shallow water with abundant emergent vegetation to open deep water with little emergent vegetation of any kind (Figs. 3, 4, and 5). Water depth at feeding site and % emergent vegetation were the 2 factors that were significant
(α = 0.05) in separating species. Species richness and density were concentrated where aquatic vegetation was most prevalent (Figs. 4 and 5). Undoubtedly factors not measured in this study, such as food types (Weller 1972), feeding behavior (Lack 1971), and other aspects of food selection also are important in separating waterfowl environments, as is evidenced in other birds (Betts 1955, Root 1969, Shugart and Patten 1972).

Certainly the niche requirements for each species will shift from season to season (Wiens 1969) and care must be taken not to generalize for waterfowl wintering grounds as a whole. In fact it would be difficult, if not impossible, to determine the niche of a species in its entirety. However, the use of multivariate statistical methods provides important progress toward this end. These procedures produced a representative characterization and interpretation of the ecological niches of wintering waterfowl. Further, application of these or similar techniques may be useful in wetland management programs. In so doing it would be difficult to manage for or against particular species within a subgroup, such as within the subgroups identified in Fig. 4, because of broad overlap in habitat use by the grouped species.

Fig. 6. Limits of the existing habitat space represented by the 95% confidence ellipse circumscribing the principal component values for the individual random samples (open circles). Mean values for the waterfowl species are superimposed (closed circles).
SUMMARY

A comparative study of the environmental relationships among 14 species of wintering waterfowl was conducted at the Welder Wildlife Foundation, San Patricio County, near Sinton, Texas during the fall and early winter of 1973. Measurements of 20 environmental factors (social, vegetational, physical, and chemical) were subjected to multivariate statistical methods to determine certain niche characteristics and environmental relationships of waterfowl wintering in the aquatic community.

Each waterfowl species occupied a unique realized niche by responding to distinct combinations of environmental factors identified by principal component analysis. One percent confidence ellipses circumscribing the mean scores plotted for the first and second principal components gave an indication of relative niche width for each species. The waterfowl environments were significantly different interspecifically and water depth at feeding site and % emergent vegetation were most important in the separation. This was shown by subjecting the transformed data to multivariate analysis of variance with an associated step-down procedure. The species were distributed along a community cline extending from shallow water with abundant emergent vegetation to open deep water with little emergent vegetation of any kind. Four waterfowl subgroups were significantly separated along the cline, as indicated by one-way analysis of variance with Duncan’s multiple range test. Clumping of the bird species toward the middle of the available habitat hyperspace was shown in a plot of the principal component scores for the random samples and individual species.

Naturally occurring relationships among waterfowl were clarified using principal component analysis and related multivariate procedures. These techniques may prove useful in wetland management for particular groups of waterfowl based on habitat preferences.

ACKNOWLEDGMENTS

This research was supported by the Rob and Bessie Welder Wildlife Foundation, Sinton, Texas (Welder Contribution No. 167). The Arkansas Audubon Society Trust Fund provided a greatly appreciated research grant. Additional thanks are extended to James E. Dunn, Alan F. Posey, Tim Mantooth, and Joel Carver for their help with statistical analysis. E. Bolen, L. Fredrickson, and L. Stickel provided critical reviews of the manuscript.

Also, sincere appreciation and gratitude is extended to Betty Jean White for her assistance in data collecting and laboratory analysis, and for her constant encouragement to the senior author.

LITERATURE CITED


REPRODUCTIVE SUCCESS AND FORAGING BEHAVIOR OF THE OSPREY AT SEAHORSE KEY, FLORIDA

ROBERT C. SZARO

Previous accounts have described the decline of reproductive success in the Osprey (Pandion haliaetus) (Ames and Mersereau 1964, Reese 1970, Wiemeyer 1971). With these reports in mind, I studied the breeding biology of Ospreys at Seahorse Key, Levy County, Florida. The principal aims of this study were to investigate the breeding biology of an Osprey population on an isolated marine island without serious pesticide problems (Blus et al. 1974). Included in the study are features of Osprey breeding behavior and feeding habits, and pesticide contents of Osprey eggs and food.

STUDY AREA AND METHODS

Seahorse Key is located approximately 4 km southwest of the town of Cedar Key on Florida’s Gulf Coast, and is approximately 9 km from the mainland. Since 1936 when Seahorse Key became incorporated into the Cedar Keys National Wildlife Refuge, the breeding Ospreys, White Ibises (Eudocimus albus), Brown Pelicans (Pelecanus occidentalis), and other forms of wildlife have been protected.

Seahorse Key consists of 62.5 ha, 20.1 of which are mangrove swamp, 15.8 are in the littoral zone below mean high tide, and 26.6 include the beaches and upland areas (Wharton 1954). The key has large areas of mangrove swamp in which many mangroves were killed by freezes in January 1960, 1963, and 1966. The mangrove swamp includes principally black mangrove (Avicennia nitida), (90-95% of the mangrove area) with some white mangrove (Laguncularia racemosa) on the northern fringes and a rare occurrence of red mangrove (Rhizophora mangle) scattered throughout the swamps (Wharton 1954). The mangrove swamps, found exclusively on the mainland side of the island and lining its northern basins (Fig. 1), are in a period of regrowth, but each year fewer and fewer of the dead mangroves are strong enough to support the weight of an Osprey nest. The littoral zone has numerous shoal areas in the northern basins and on the southern side of the island that are used for fishing by the Ospreys. In addition, the east and west banks on the southern side of the key are heavily used by feeding Ospreys.

During the 1972 breeding season I checked each Osprey nest at least weekly, beginning on 6 March 1972 and ending on 30 July 1972. Nests were examined either by climbing or with the aid of a mirror on a long pole. Active nests were defined as those nests with eggs or, in those nests not readily observable, by the presence of young at the nest. Nest height from the ground or to sea level was measured with a steel tape and a mean height and standard deviation calculated.

Information on Osprey foraging behavior was obtained with binoculars and a stopwatch. Each fishing effort was timed from the moment an Osprey first was sighted until it captured a fish or was lost from view. Fishing efficiency was determined by the percent of fishing attempts resulting in fish capture.

Three eggs, each containing a rotten but well developed embryo, were taken from Osprey nests after these eggs had exceeded the normal incubation period by at least a

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week. Along with the eggs, 3 fish, somewhat dehydrated, were also retrieved from the same nests. Samples of fish muscle and homogenized egg contents were separately ground with sodium sulfate. Subsequently each sample was extracted with petroleum ether in a Soxhlet apparatus for 8 h. followed by acetonitrile partitioning and florisil clean-up. Using the silica gel-pentane separation technique of Snyder and Reinert (1971), the resulting sample was treated for the separation of polychlorinated biphenyls (PCB's) from DDT and its metabolites, and dieldrin. Analysis for the DDT components and dieldrin was performed on a Varian Aerograph model 600-D gas chromatograph using a column of OV 210 (6.4%) and OV 17 (1.6%) and operated isothermally (oven and detector at 209°C). The PCB analysis was performed on a Varian Aerograph model 2100 gas chromatograph using a similar column and operated with the oven at 206°C and the detector at 218°C.

RESULTS AND DISCUSSION

Reproduction.—During 1972 the 20 Osprey nests on Seahorse Key ranged in height from 2 to 14 m ($\bar{x} = 6.1 \pm 3.2$ m) with 85% of the nests on the north side of the Key (Fig. 1). The major factor determining Osprey nest height was the height of the dead black mangroves as 75% of the nests were in mangroves. Sixteen of the nests were below 8 m in height. The four
nests above 3.0 m in height were in living oak (*Quercus virginiana*) or cedar (*Sabina silicicola*). Two of these nests were inactive by 26 March 1972. Three nests in the mangroves were inactive by 3 April 1972; the remaining 15 nests were classified as being active.

Six closely observed nests had 3 eggs each with a hatching success of 44%. Three of the resulting hatchlings were lost in early May when 2 nest sites were destroyed by a storm. Eight of the 15 active nests produced a total of 11 fledglings.

Henny and Wight (1969) stated that each adult female in an Osprey population must produce between 0.95 and 1.30 young per nest each year in order to maintain a stable population. The 1972 production level at Seahorse Key of 0.73 young per nesting female was below that needed for a stable population. However, if not for the storm in May, production would have been 0.93 young per nesting female.

Foraging.—The Osprey preferred the shallow waters afforded by low tide for fishing. The birds fed mainly during the middle-late ebbing to the middle rising of the tide in the Cedar Keys area. They showed a definite preference for the shoal areas consisting of the East and West Banks and the shallow areas on the south side of the Key. The northern basins were used for fishing but not as extensively as the fishing grounds on the south side. The shallower waters in these areas before and after low tide were likely favorite areas for fishing because of the large numbers of speckled trout (*Cynoscion nebulosus*) and striped mullet (*Mugil cepalus*) that frequent them.

Despite their quick plunges, Ospreys required several strikes and many minutes to catch a fish (Table 1). Overall, adult Ospreys were successful in 58% of their fishing efforts. Ueoka and Koplin (1973) found that adult Ospreys in northwestern California were successful in 82% of their fishing efforts. At Seahorse Key, fish capture by adult Ospreys occurred on the first attempt in 52% of the 23 successful fishing efforts. Of the 17 unsuccessful fishing efforts, 7 (41%) involved Ospreys that flew back to the key without securing fish. The remaining 10 (58%) unsuccessful fishing efforts involved birds that were lost from view.

During the first week of flying, the young followed the adults to the shoal areas and attempted to fish for themselves. Twice adults used food as a method of coaxing the young to feed for themselves. An adult, carrying a fish, flew around the young and finally dropped it in mid-air, making it necessary for the young bird to dive quickly in order to catch it before it hit the water. In this manner the young were forced to retrieve the fish from the surface of the water until they finally started fishing by themselves.
Table 1

Analysis of Fishing Efficiency of Adult and Fledgling Ospreys

<table>
<thead>
<tr>
<th></th>
<th>Adult</th>
<th>Young</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. fishing efforts</td>
<td>40</td>
<td>21</td>
</tr>
<tr>
<td>No. fish caught</td>
<td>23</td>
<td>6</td>
</tr>
<tr>
<td>Percent of fishing efforts successful</td>
<td>57.5</td>
<td>28.6</td>
</tr>
<tr>
<td>Attempts/catch</td>
<td>5.4 ± 6.7*</td>
<td>12.7 ± 7.2</td>
</tr>
<tr>
<td>Minutes/catch</td>
<td>38.3 ± 21.7*</td>
<td>77.3 ± 32.8</td>
</tr>
<tr>
<td>Percent of attempts resulting in a catch</td>
<td>18.6</td>
<td>6.3</td>
</tr>
</tbody>
</table>

* Mean ± standard deviation; Significant difference between adults and young at P ≤ 0.05 using Student’s T Test.

This account is similar to that of Meinertzhagen (1954) for the luring of young Ospreys to fish on their own.

Recently fledged Ospreys were less efficient at fishing than their parents. The young birds made more attempts and required a longer period of time to catch a fish than their more experienced parents (Table 1).

Ospreys at Seahorse Key fed primarily on speckled trout; of 103 food items identified, 64% were speckled trout. Of the remaining fish caught, 27% were striped mullet, 8% were sea catfish (Galeichthys felis), and 2% were ocellated flounder (Amclopsetta quadrocellata).

Eggshell thickness.—Seven samples of Osprey eggshells were obtained and sent to D. W. Anderson for measurement. The shells ranged in thickness from 0.38 to 0.53 mm with an average thickness of 0.46 ± 0.06 mm. Membrane thickness was 0.12 ± 0.01 mm with extremes of 0.11 and 0.14 mm. The calcite layer had an average thickness of 0.34 ± 0.06 mm with the values ranging from 0.24 mm to 0.40 mm.

Anderson (pers. comm. in 1972) reports a “normal” value for Osprey eggshell thickness as 0.50 ± 0.01 mm in 20 eggs from Florida (specific location and dates not provided). The mean membrane thickness was 0.13 mm, and the mean calcite layer thickness was 0.37 mm. Prior to 1947 average shell thickness in Eastern United States Ospreys was 0.505 ± 0.004 mm (Anderson and Hickey 1972). These data suggest that Osprey eggs at Seahorse Key were 8 to 9% thinner than “normal,” though interpretation of shell thickness is made difficult by lack of knowledge concerning stage of embryo development of eggs measured.

Pesticide analyses.—Three Osprey eggs and 3 fish samples taken from active nests were analyzed on a lipid weight basis to determine organochlorine pesticide and PCB residues. The eggs contained an average concentration of 8.34 ± 1.45 ppm of p,p’-DDE, 3.55 ± 0.24 ppm of p,p’-DDD, 0.30 ± 0.02
ppm of \textit{p,p'-DDT}, 0.26 ± 0.02 ppm of \textit{dieldrin}, and 29.9 ± 6.7 ppm of \textit{PCB} (Aroclor 1254). The fish contained low levels of organochlorines and only one, a sample of ocellated flounder contained high levels of PCB's (Table 2).

Pesticide and PCB burdens in Osprey eggs and their food fishes have been reported by several investigators (Dustman et al. 1971, MacCarter et al. 1969, Stickel et al. 1965, Wiemeyer et al. 1975). DDE residues found in Connecticut Osprey eggs were 254 ppm (lipid weight) (converted from wet-weight by using the fact that fresh Osprey eggs contain up to 3.5% lipid, Wiemeyer pers. comm.), and in Maryland Ospreys DDE residues were 69 ppm, (lipid basis). Residues in eggs from Seahorse Key were much lower than these. Similarly, Connecticut Osprey eggs contained an average of 17 ppm (lipid weight basis) of \textit{dieldrin} as compared to only .26 ppm \textit{dieldrin} in Seahorse Key Osprey eggs. Dustman et al. (1971) reported a median concentration of PCB's of 15.9 ppm (wet-weight basis) (approximately 454 ppm on a lipid basis) from eggs in Connecticut. Thus the 3 Osprey eggs from Seahorse Key contained low pesticide and PCB burdens.

Duke et al. (1970) report Aroclor 1254 from the water, sediment, and biota of Escambia Bay, Florida. The Aroclor content in the water from Escambia Bay was < 1 ppb. Their study showed biological magnification of Aroclor 1254 in a food chain: sediment contained < 0.3–1.7 ppm; crustaceans contained 1.0–7.0 ppm; fish contained 415–184 ppm. It is of interest to note that the PCB concentrations of their fish (including species examined in the present study) were similar to those in the fish taken from Osprey nests at Seahorse Key (Table 2).

There is, finally, no concrete evidence to suggest that any of these chlorinated hydrocarbon residues played any significant role in influencing hatching success of these birds especially since eggshell thicknesses of these birds were near "normal."
SUMMARY

During 1972 there were 15 active Osprey nests on the 62.5 ha of Seashorse Key, Florida. The Osprey population on this key produced 0.73 young per nesting female which is below the 0.95 to 1.30 young per nesting female necessary to maintain a stable population. Adult Ospreys were successful in 18.6% of their fishing attempts. The fishing technique of the Osprey is at least a partially learned behavior: adults required only 5.4 attempts per catch and 38.3 min per catch, but the young required 12.6 attempts and 77.3 min per catch.

Pesticide analyses of 3 osprey eggs indicated low levels of organochlorines and PCB's. Eggshells ($n = 7$) were approximately 9% thinner than shells collected prior to 1947.

ACKNOWLEDGMENTS

I thank David W. Johnston for his generous help throughout my study and Pierce Bredkorb, Carmine Lanciani, John Ogden, and Stan Wiemeyer for their review of my manuscript. I am grateful to Edward Collinsworth for granting me a permit to work on Seashorse Key. A. D. Folks assisted me in travelling back and forth to Seashorse Key and Frank Maturo provided living quarters and an outboard motor boat at Seashorse Key. Research support was provided by the University of Florida, Department of Zoology and from an Estuarine Ecology Grant through the Division of Biological Sciences. I am grateful to Daniel Anderson for measuring my eggshell samples and Ronald Bull for his assistance in the pesticide analyses.

LITERATURE CITED


**REQUEST FOR ASSISTANCE**

*Purple Martin color-marking.*—A large scale continent-wide Purple Martin color-marking project was initiated in 1977. Observers are asked to look for and report any color-marked (plastic leg bands and/or wing tags) Purple Martins. Please record the color of the bands or wing tags, which leg they are on, age and/or sex (if either is known), where and when observed, and whether the bird was in a roost, staging flock, migratory flock, or at a nest site (scouting or nesting?). We are especially interested in the movements of young birds and their return to the parent colony or nearby colonies. All reports will be acknowledged and should be sent to Ms. Kathleen Klimkiewicz, Bird Banding Laboratory, Laurel, Maryland 20811.
GENERAL NOTES

Changing avian community structure during early post-fire succession in the Sierra Nevada.—In August 1960 an intense fire consumed over 15,800 ha of pine-fir forest in the northern Sierra Nevada near Truckee, Nevada Co., California. Establishment in 1965 of 2 permanent study plots led to a comparison of breeding bird populations in burned and adjacent unburned habitats between 1966 and 1968 (Bock and Lynch, Condor 72:182-189, 1970). In 1975 we had the opportunity to census these areas after 7 years of further post-fire succession. The purpose of this note is to describe bird species diversity and avian community structure as they changed between 1968 and 1975.

Study areas.—This work was conducted at the University of California’s Sagehen Creek Field Station, located 19 km N of Truckee. Each study plot was 8.5 ha, gridded with permanent steel fenceposts set at 20 m intervals. The unburned plot is a mature pine-fir forest, dominant species being Jeffrey pine (Pinus jeffreyi) and white fir (Abies concolor). The burned plot contains a few scattered mature trees spared by the fire (including some Pinus ponderosa as well as A. concolor and P. jeffreyi), and especially brush species such as Ceanothus velutinus and Arctostaphylos patula. There are substantial numbers of young pine. Between 1968 and 1975 there was a marked decrease in standing dead timber and an increase in brush. For more detailed descriptions of the vegetation, see Bock and Lynch (1970) and Bock et al. (Proc. Tall Timbers Fire Ecol. Conf. 14:195-200, 1974).

Census methods.—The census technique used was the Williams spot-mapping method (Williams, Ecol. Monogr. 6:317-408, 1936). This approach to estimating absolute densities involves the repeated location of breeding birds on a grid, with clusters of observations eventually revealing the presence and territory sizes of breeding pairs. A major problem with this method appears to be that different interpretations can be given to a particular data set by different individuals (Best, Auk 92:452-460, 1975). Since all density estimations in this study were made by 1 person (CEB), and since accurate relative abundances of species are sufficient for calculation of diversity and similarity indices in any event, we feel that the technique was valid in this instance. The avifauna of the unburned forest should have changed little over the 7-year period. Similarity of census results on the unburned plot in 1968 and 1975 (Table 1) supports our confidence in all of the data collected.

Censuses were conducted from late May until early July, and varied from 1 to 3 h in 1968 and from 2 to 4 h in 1975. Numbers of censuses were as follows: 1968 unburned plot—15; 1975 unburned plot—11; 1968 burned plot—21; 1975 burned plot—11. Bock and Lynch (1970) include some detailed information on our particular approaches to the spot-mapping method.

Results.—Table 1 is a summary of the census data for bird populations on the burned vs. unburned study plots. Densities are expressed as pairs per 40.5 ha (100 acres) to conform with most similar studies. Species richness, species diversity, and evenness all were highest on the burned plot in 1968, lowest on the burn in 1975, and intermediate on the unburned plot in both years. Although some of these differences are minor, diversity on the burned plot was considerably higher in 1968 than in 1975.

Table 2 is a series of similarity indices comparing species densities on the plots in 1968 and 1975. Two obvious trends emerge from these data. First, within-plot comparisons (A, B) show that there was a much greater change over 7 years on the burned plot compared to the unburned forest. Obviously this is a reflection of relatively rapid and
<table>
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<th>Species</th>
<th>Burned plot</th>
<th>Unburned plot</th>
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<tr>
<td>Common Flicker (Colaptes auratus)</td>
<td>3.6</td>
<td>2.4</td>
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<tr>
<td>Yellow-bellied Sapsucker (Sphyrapicus varius)</td>
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<td>1.2</td>
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<td>Williamson's Sapsucker (S. thyroideus)</td>
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<td>2.4</td>
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<td>White-headed Woodpecker (Picoides albolarvatus)</td>
<td>1.2</td>
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<tr>
<td>Hairy Woodpecker (P. villosus)</td>
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<td>1.2</td>
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<tr>
<td>Three-toed Woodpecker (P. arcticus)</td>
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<td>Empidonax sp.</td>
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<td>Western Wood Pewee (Contopus sordidus)</td>
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<tr>
<td>Olive-sided Flycatcher (Nuttalornis borealis)</td>
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<td>1.2</td>
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<tr>
<td>Steller's Jay (Cyanocitta stelleri)</td>
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<td>Mountain Chickadee (Parus gambeli)</td>
<td>4.8</td>
<td>7.2</td>
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<td>White-breasted Nuthatch (Sitta carolinensis)</td>
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<td>American Robin (Turdus migratorius)</td>
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<td>Hermit Thrush (Catharus guttatus)</td>
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<td>Mountain Bluebird (Sialia currucoides)</td>
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Table 1 Continued

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<td>Townsend’s Solitaire (Myadestes townsendi)</td>
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<td>Cassin’s Finch (Carpodacus cassini)</td>
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<tr>
<td>Pine Siskin (Carduelis pinus)</td>
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<tr>
<td>Red Crossbill (Loxia curvirostra)</td>
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<tr>
<td>Green-tailed Towhee (Pipilo chlorura)</td>
<td>2.4</td>
<td>9.6</td>
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<tr>
<td>Dark-eyed Junco (Junco hyemalis)</td>
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<td>Fox Sparrow (Passerella iliaca)</td>
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<td>29.9</td>
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<td>Totals</td>
<td>109.2</td>
<td>104.1</td>
<td>110.9</td>
<td>102.0</td>
</tr>
</tbody>
</table>

Species Richness

Species Diversity

Evenness

---

* These 2 species probably were not breeding but were observed feeding on the unburned plot in 1975 with such regularity that we have included them in the table at low densities. Their inclusion has little effect on overall density or species diversity measurements.

b \( H' = -\sum_{i=1}^{S} p_i \log_2 p_i \) (see Peet, Annu. Rev. Ecol. Syst. 5:285-307, 1974).

c \( J = H'/H_{max} \) (see Peet 1974).
Table 2

Similarities Between the Breeding Avifaunas of Burned and Unburned Plots in 1968 and 1975

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Percent similaritya</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Unburned (1968) vs. unburned (1975)</td>
<td>83</td>
</tr>
<tr>
<td>B. Burned (1968) vs. burned (1975)</td>
<td>54</td>
</tr>
<tr>
<td>C. Burned (1968) vs. unburned (1958)</td>
<td>47</td>
</tr>
<tr>
<td>D. Burned (1975) vs. unburned (1975)</td>
<td>28</td>
</tr>
</tbody>
</table>


dramatic successional events in the post-fire community. Second, and perhaps less expected, is the observation that breeding bird populations of the burned and unburned forest were more similar in 1968 than they were in 1975 (Table 2, C and D). That is, the 2 avian communities lost rather than gained similarity over the 7-year period.

Discussion.—In some respects the burned plot more closely resembled an unburned forest in 1968 than it did in 1975. This fact may explain most of our findings, since it is generally agreed that avian species diversity and community composition are tied to habitat structure (e.g., MacArthur, pp. 189–221, in Avian Biology Vol. I, Farmer and King eds., Academic Press, N.Y., 1971). In 1968, 8 years after the fire, there were numerous standing dead trees; there was much open ground, just as there is in an unburned forest. By 1975 the burned plot was well on its way to being a dense brushfield, with many fewer standing dead trees. Bird species characteristic of brush stands in the area (Yellow Warbler, Green-tailed Towhee, Fox Sparrow) increased dramatically on the burned study plot between 1968 and 1975. Open-ground foragers (American Robin, Mountain Bluebird, Dark-eyed Junco) declined (Table 1). Six of 11 hole-nesting species decreased on the burn between 1968 and 1975, while only 1 increased. This species was the Mountain Chickadee, which appeared to forage extensively in the stands of young regenerating pine on the burned plot.

Most, but not all, of the declining similarity between the burned and unburned plot avifaunas was the result of population changes in the Dark-eyed Junco and Fox Sparrow. These were the most abundant species on the burn in 1968 and 1975, respectively. Juncos also were very common in the unburned forest, nesting largely on the ground and foraging on the forest floor. In 1968 juncos were similarly abundant on the burn (Table 1). By 1975 the brushfields had closed off much of the burn and Fox Sparrows replaced juncos as the most abundant breeding birds.

Oдум (Ecology, 2nd ed., Holt, Rinehart, and Winston, New York, 1975:155) states that "those species that are important in the pioneer stages are not likely to be important in the climax." Our findings do not support this generalization. It appears that bird species populations changed on the burn in response to modifications of their individual habitat requirements. In some instances this resulted in convergence of the 2 avifaunas, while in others it caused a decreased similarity between burned and unburned plot population levels. This is suggestive of the individualistic concept of community organization proposed by Gleason (Am. Midl. Nat. 21:92–110, 1939).

Beaver (Ph.D thesis, Univ. Calif., Berkeley, 1972) studied patterns of avian species diversity in the Sagehen Creek Basin, where this study was conducted. He compared 3 successional stages—brush, brush-conifer, and coniferous forest—and found that diver-
sity increased with habitat age. Examination of the data analyzed by Beaver (1972) makes it apparent that only by 1975 was our burned study plot beginning to resemble his earliest or “brush” stage of succession, and to support a similar breeding avifauna. It would appear that there exists an earlier “pre-brush” period of higher bird species diversity, followed by a decline when dead trees fall, when brush species become dominant, and when as a result there is much structural simplification of the post-fire community.

Vernon Hawthorne, Starker Leopold, and Marshall White generously made available the facilities of the Sagehen Creek Field Station. This study was supported in part by a grant from the University of Colorado Council on Research and Creative Work.—CARL E. BOCK, MARTIN RAPHAEL, and JANE H. BOCK, Dept. of Environmental, Population, and Organismic Biology, Univ. of Colorado, Boulder 80309 (CEB, JHB), and Dept. of Forestry and Conservation, College of Natural Resources, Univ. of California, Berkeley 94720 (MR). Accepted 7 Dec. 1976.

Notes on the distribution of birds in Sonora, Mexico.—Over the past several years we have made observations of birds in northwestern Mexico that supplement published distributional accounts. Many other individuals have contributed significant observations in Sonora to us, so that we are able to elaborate on the status of 65 species of birds, including 20 species new for the state. Van Rossem (Occas. Papers Mus. Zool. Louisiana State Univ. 21:1–379, 1945) prepared the only major work on the birds of Sonora. Friedmann, et al. (Pac. Coast Avif. 29, 1950) and Miller, et al. (Pac. Coast Avif. 33, 1957) are authors of the most recent check-lists covering the area and provide the basis for deciding what distributional data should be included in this paper. At least 2 recent works on Mexican birds (Alden, Finding the Birds in Western Mexico, Univ. Ariz. Press, Tucson, 1969; Peterson and Chalif, A Field Guide to Mexican Birds, Houghton Mifflin Co., Boston, 1973) cited Sonora in ranges of certain species for the first time but without locality or details; we document some of the reports on which these accounts are based.

Sonoran localities mentioned in the species accounts may be found on the map (Fig. 1). Where specimens have been taken, we have indicated their present location as follows: Amadeo M. Rea Collection, Tucson, Az. (AMR), Delaware Museum of Natural History, Greenville (DMNH), Museum of Vertebrate Zoology, Berkeley (MVZ), University of Arizona, Tucson (UA), University of California at Los Angeles (UCLA). Important sight records are identified by the initials of the observer(s) as listed in the acknowledgments. Our own observations are identifiable by our initials or by the use of the word “we.”

**Common Loon** (*Gavia immer*).—Zimmerman and Boet ether (Condor 69:527, 1967) summarized Mexican records of this species and reported the first specimen from Mexico (excluding Baja California). This loon is a common winter visitor along the coast of Sonora with observations from 23 September to 28 April. Most March and April birds are in breeding plumage. Two birds found dead on the beach 4 December 1965 near Puerto Peñasco were preserved (UA); this date is 1 week later than the specimen reported by Zimmerman and Boet ether.

**Red-throated Loon** (*Gavia stellata*).—Van Rossem (op. cit.) gave only 2 records from the Gulf of California. Additional sightings are from 26 km SSE of La Libertad 27 November 1970 (SR), and Puerto Peñasco 15–18 March 1962 (SD), and 22 February 1975 (DS).

**Horned Grebe** (*Podiceps auritus*).—Earlier writers did not report this species from Mexico at all, but Peterson and Chalif (op. cit.) referred to it as “casual” in Sonora.
It appears to be rare, though possibly overlooked and specimens are lacking. Sightings are from Puerto Peñasco (23 October 1964, 3 birds WB, SR; 31 October 1970, 2 birds RW), Punta Santa Rosa (29–30 November 1974, 2 birds SM), and Bahía Kino (21–23 February 1969, EC).

Northern Fulmar (Fulmarus glacialis).—Two dark phase birds, carefully noted 24 March 1968 at Puerto Peñasco (William Bolte and RLC), constitute the only observation in Sonora.

Green Heron (Butorides striatus).—Van Rossem (op. cit.) had many summer records but only 1 in winter. We found it in the mangroves at Punta Santa Rosa from September through February. It has also been reported on the Sonoyta River in December (RLC).
Little Blue Heron \textit{(Florida caerulea).}—The species was listed by Van Rossem (op. cit.) as a summer visitor north to Guaymas with 1 winter record from Tiburón Island. There are winter observations in mangroves at Punta Santa Rosa (16 December 1973, DL, SR) and Bahía Kino (21–23 February 1970, WH, GB).

Reddish Egret \textit{(Dichromanassa rufescens).}—Recorded by van Rossem (op. cit.) south of Tepoca. This egret is a regular fall and winter visitor in small numbers along the Gulf coast as far north as Puerto Peñasco (extreme dates, 7 September and 14 April).

Louisiana Heron \textit{(Hydranassa tricolor).}—Van Rossem (op. cit.) listed it as an uncommon resident from Guayas southward. Currently it is a common visitor along the coast throughout the year. Observations of up to 6 birds together extend north to Puerto Peñasco and are mostly between 7 September and 25 April.

Least Bittern \textit{(Ixobrychus exilis).}—We took 2 specimens (UA), a male (wt. 64 g) with whitish irides on 8 September 1973 and the other a female (81 g) with yellowish-white irides on 17 September 1974, at Punta Santa Rosa. R. W. Dickerman had identified them as \textit{I. e. pullus}, the first from Sonora since the type series (van Rossem, Trans. San Diego Soc. Nat. Hist. 6(15):227–228, 1930). Both of our birds were captured in mist nets set in mangroves (\textit{Avicennia germinans}, \textit{Laguncularia racemosa}).

The birds did not have active gonads and we have no evidence that the species nests at Punta Santa Rosa. We banded and released an additional adult at the same locality 18 August 1975.

White Ibis \textit{(Eudocimus albus).}—Van Rossem (op. cit.) cited 1 record north of Guaymas. Recent sightings are from Bahía Kino (21–23 February 1969, EC), Punta Santa Rosa (18 January 1974, DL, SR), and north of Puerto Peñasco (7 May 1975, SL).

Roseate Spoonbill \textit{(Ajaia ajaja).}—Van Rossem’s (op. cit.) most northerly point of record was Bahía Kino (September). One was seen 26–27 June 1973 at Punta Santa Rosa (JCL, DL). Inland, we saw 3 adults with Snowy Egrets (\textit{Egretta thula}) on flooded fields at Bamori on 9 September 1973.

Brant \textit{(Branta bernicla nigricans).}—Grinnell (Univ. Calif. Publ. Zool. 32, 1928) recorded the Black Brant as a common winter visitor along the Pacific coast of Baja California, but mentioned only a single “not quite conclusive” record for Gulf waters. There are no published records from elsewhere in western Mexico. In recent years there has evidently been a substantial shift in the wintering grounds of this subspecies. Since 1970, flocks of brant have been seen regularly in winter (November–February) at Bahía Kino and Punta Santa Rosa. Usually these groups number 150–450 birds, but about 2000 were observed in November (GM). Single birds have also been seen elsewhere; one 8 June 1973 at La Libertad (JHL) and 1 or 2 on 23–31 March 1974 at Puerto Peñasco (JW, RW).

Common Goldeneye \textit{(Bucephala clangula).}—Booth (Condor 55:160, 1953) reported on a pair seen at Guaymas in February 1951. The only additional records are sightings by different observers from 9 November to 30 March from Puerto Peñasco, Bahía Kino, and Guaymas. No more than 4 birds were seen on any occasion.

Oldsquaw \textit{(Clangula hyemalis).}—Huey (Trans. San Diego Soc. Nat. Hist. 5:11–40, 1927) observed 1 bird in the Gulf near San Felipe, B.C. on 1 April 1926, but Friedmann et al. (op. cit.) did not list it in Mexico. Peterson and Chalif (op. cit.) listed it as accidental in the Gulf of California. A male was seen on 28 November 1970 at Tepoca (WC, DL, SR).

White-winged Scoter \textit{(Melanitta deglandi).}—One was seen at Puerto Peñasco 1 April 1973 (SD et al.) and reported by Monson (Am. Birds 27:803–806, 1973). Another was seen at the same locality 22–23 February 1975 (DS). Grinnell (op. cit.) listed it from
the Gulf side of Baja California and Friedmann et al. (op. cit.) reported it only from Baja California.

**Rough-legged Hawk** (*Buteo lagopus*).—Only Peterson and Chalif (op. cit.) and Davis (A Field Guide to the Birds of Mexico and Central America, Univ. of Texas Press, Austin, 1972) list it, as a rare or occasional straggler to northern Mexico. Two adult light-phase birds were noted 6 January 1973, 21 km south of Nogales at an elevation of about 1100 m (PA). Another, also close to the border, was seen 16 February 1973 (WR), less than 2 km north of Cananea (Monson, Am. Birds 27:646-650, 1973).

**Ferruginous Hawk** (*Buteo regalis*).—This hawk has been seen frequently at Puerto Peñasco with observations from 23 October to 2 March in all months except February (PA, WB, RLC, SM, DS, JW, RW), but is unreported in the literature for northwestern Mexico.

**Sandhill Crane** (*Grus canadensis*).—Van Rossem (op. cit.) reported it as formerly abundant in the Colorado River delta and Rio Mayo valley but indicated that numbers were greatly reduced at the time of his writing. The only recent observations were about 200 seen 19 January 1974, in an agricultural area 60 km WSW of Hermosillo by R. Craig and 2 on 13 October 1971 at a dam on the San Pedro River near Cananea (SS, ES).

**Virginia Rail** (*Rallus limicola*).—A specimen (wt. 55 g; UA) taken in the mangroves at Punta Santa Rosa 17 September 1974 was in fresh plumage. Cunningham saw 1 bird 23 December 1968 on the Sonoyta River close to the Arizona border. Van Rossem (op. cit.) cited only 1 Sonoran specimen but considered it possibly resident in extreme northern Sonora, as did Friedmann (op. cit.).

**Black Oystercatcher** (*Haematopus bachmani*).—Three were found in March and 1 in May 1970 at Puerto Peñasco (SD). Friedmann (op. cit.) reported it only from the Pacific side of Baja California.

**Piping Plover** (*Charadrius melodus*).—Five of these plovers were observed at Puerto Peñasco 17 April 1965 (SR), and another was noted (JW, RW) there 27 November 1971 (Monson, Am. Birds 26:100-104, 1972). Four individuals were watched at Puerto Peñasco on 28 February 1972 (PJ, RLT, RW) and reported by Monson (Am. Birds 26:638-642, 1972). The species is not otherwise known from western Mexico.

**Mountain Plover** (*Charadrius montanus*).—Van Rossem (op. cit.) cited 3 Sonoran records, only 1 subsequent to 1900. At Cerro Colorado, in the Sierra Pinacate, 3 groups totalling 45 birds were observed 22 November 1973 (DL, SR), in a flat shrubless area dominated by bare ground and supporting only scattered small plants of *Cryptantha* sp., *Dalea* (probably *mollis* or *neomexicana*), *Calodendron* Palmeri and *Euphorbia polyacarpa*.

**Upland Sandpiper** (*Bartramia longicauda*).—One seen in grasslands about 16 km S of Benjamin Hill 31 July and 8–9 August 1969 (RET) constitutes the only observation of the species in Sonora.

**Wandering Tattler** (*Heteroscelus incanus*).—Van Rossem (op. cit.) noted only 1 individual (seen 21 April 1930) in Sonora. Friedmann (op. cit.) reported it from Sonora without comment. The species was seen 22 April 1966 (DL) and 23 April 1974 (JW, RW) at Puerto Peñasco.

**Red Knot** (*Calidris canutus*).—Although cited few times in the literature, this species is evidently a regular spring and fall migrant and winter visitor along the coast, sometimes in numbers (over 100 at Puerto Peñasco, 13 April 1973, SL). Records from Puerto Peñasco and Bahía Kino extend from 25 September to 28 April.

**Stilt Sandpiper** (*Micropalama himantopus*).—We saw 1 on flooded fields at Bamori 9 September 1973. There are no published records of this species in Sonora.

**Pomarine Jaeger** (*Stercorarius pomarinus*).—The species is unreported from Sonoran
waters. On 11 April 1976, Arnold R. McGill saw 2, 1 harassing an Elegant Tern (*Sterna elegans*), close to shore at Bahía Kino.

**Parasitic Jaeger** (*Stercorarius parasiticus*)—The only observation of this species in Sonora is that of 1 light-phase adult seen 29 December 1974 at Puerto Peñasco (DS).


**Sabine’s Gull** (*Xema sabini*)—The only Sonoran reports are from Puerto Peñasco, 3 birds 5–6 October 1959 (RLC) and an immature 13 October 1969 (RLC).

**Common Tern** (*Sterna hirundo*)—Although unreported in the literature from Sonora, it may be a common transient at Puerto Peñasco. Many flew south past there 14 July 1968 (DL) and 120 (including immatures) passed in 4.5 hours on 13 October 1969 (RLC). One bird was noted 24 March 1968 (RLC). There is one winter record, 3 January 1965 (RSC). A specimen (UA) was taken 25 September 1965. We know of only one observation further south, a single bird at Punta Santa Rosa 11 October 1973 (DL, SR).

**Least Tern** (*Sterna albinodis*)—Reported by van Rossem (op. cit.) as a summer visitor from Guaymas southward. There is a small nesting colony at Puerto Peñasco but no specimens have been taken and the subspecies is hence uncertain. Birds arrive at the end of March and are present in April (GG, FT, JJL, DL), nesting in June (RW), and absent by 13 July (DL). There are a number of records of migrating birds (April and August–September) from coastal localities.

**Black Tern** (*Chlidonias niger*)—Phillips and Amadon (Condor 54:163–168, 1952) collected the only specimen of the Black Tern from Sonora near Caborca on 31 October 1948 but there are many observations between 13 July and 31 October from coastal localities. The only spring observation was one bird 28 April 1972 at Bahía Kino (GM).

**Black Skimmer** (*Rynchops niger*)—This species has not previously been reported north of Guaymas. One was seen at Puerto Peñasco on 24 April 1974 (JW, RW).

**Long-eared Owl** (*Asio otus*)—The species has been found in Sonora only on Tiburon Island in late December 1931 (van Rossem, op. cit.) and at Puerto Peñasco 23 October 1964 (WB) in a grove of widely spaced, small (3 m) mesquite (*Prosopis*) trees.

**Buff-collared Nightjar** (*Caprimulgus ridgwayi*)—Even though this nightjar has been recorded in both Arizona and New Mexico, there are no published records for northern or central Sonora. We are aware of only 2 reports. Phillips and van Rossem found several individuals calling and feeding on hillsides at El Gavilan on 4–5 May 1947 and collected 2 (DMNH, UCLA). They heard others on 5 May 8 km E of Mazocahui. On 9 July 1974, several were heard (SA, TJ, SS) calling between Mazocahui and Moctezuma (Alden and Mills, Am. Birds 28:933-935, 1974).

**Lucifer Hummingbird** (*Callithorax lucifer*)—We found female Lucifer Hummingbirds common in Arroyo Cajón Bonito (1280 m) on 16 May 1976 where they foraged from the stream up the slopes. Four nests were all in the flood plain; 2 on small drooping sycamore branches (3 and 4 m above the ground) each contained 2 eggs as did another 4 m in a hackberry (*Celtis*). The fourth was under construction 2.5 m above the ground in an ash. We saw no males, although 30 females were counted in a 3 km transect of the canyon. The only other hummingbirds present were many Broad-billed (*Cynanthus latirostris*), at least 2 Broad-tailed (*Selasphorus platycercus*), and 1 Black-chinned (*Archilochus alexandri*) and nesting Blue-throated (*Lampornis clemenciae*). On 13 July, no Lucifer Hummingbirds were found in the canyon but 2 males and a female were noted.
(GM, SR) on the dry upper slopes (1550 m) where most *Agave* had completed flowering. The canyon floor, where Lucifer Hummingbirds dominated in May, now had many nesting Broad-billed, Black-chinned, and Violet-crowned hummingbirds (*Amazilia verticalis*). The species has not been reported previously from Sonora but has recently been found nesting in Arizona (Monson, Am. Birds 27:803–806, 1973).

**Allen’s Hummingbird** (*Selasphorus sasin*).—We collected a female (UA; rectrix 5 is 2.2 mm wide and tip of rectrix 2 is not emarginate) in the mangroves at Punta Santa Rosa 28 February 1971. Phillips (Condor 77:196–205, 1975) cited only 1 Sonoran specimen, a male taken near Sonoyta, also in late February.

**Calliope Hummingbird** (*Stellula calliope*).—The only known observation in a coastal locality was of a male at Bahia Kino 28 April 1972 (GM); the species is not an uncommon migrant in the eastern part of the state (van Rossem, op. cit.).

**Green Kingfisher** (*Chloroceryle americana*).—This kingfisher is widely distributed in the interior of Sonora but there are only 3 observations from coastal localities north of Agiabampo. A male was collected at Tepoca 2 January 1932 (van Rossem, op. cit.). One was seen (SD) at Puerto Peñasco on 1 April 1973 (Monson, Am. Birds 27:803–806, 1973). We banded a male in the mangroves north of Chueca on 18 September 1974.

**Williamson’s Sapsucker** (*Sphyrapicus thyroideus*).—A male was found (ES, SS) in the mountains (1800 m) near Cananea 13 October 1971 (Monson, Am. Birds 26:100–104, 1972). Van Rossem (op. cit.) cited only 1 Sonoran record.

**Tropical Kingbird** (*Tyrannus melancholicus*).—Both van Rossem (op. cit.) and Miller et al. (op. cit.) considered the northern coastal limit at Guaymas. The species is a regular summer resident in mangroves north to Tepoca, with extreme dates of 28 April and 19 August.

**Scissor-tailed Flycatcher** (*Muscicora forficata*).—We watched 1 individual on a powerline with migrating kingbirds 10 October 1973 about 26 km south of Nogales, the only observation in Sonora.

**Hammond’s Flycatcher** (*Empidonax hammondii*).—The species is a regular transient through the mountains of eastern Sonora (van Rossem, op. cit.): a male collected (UA) in mangroves at Punta Santa Rosa on 7 September 1973 constitutes the only coastal record (DL, SR).

**Horned Lark** (*Eremophila alpestris*).—We observed adults with recently fledged young in the *Salicornia* dominated flats near the beach at Tepoca on 14 April 1973. We saw a bird in the same locality on 16 July 1975 and 7 on 18 August 1975. No specimens were taken and the subspecific affinities of these birds are unknown; the locality is the southernmost known one for the species in Sonora. Previously the species had been found only as far south as Altar, where non-breeding birds were collected (Phillips and Amador, op. cit.).

**Mangrove Swallow** (*Tachycineta albilinea*).—The species is common along the coast and a few kilometers inland as far north as Desemboque; northernmost records are from 8 km SSE of La Libertad. It arrives in mid-March and nests in cardons (*Pachycreus pringlei*) in April and May. Most birds leave in mid-summer though there was an observation of 1 at San Carlos on 21 October 1975 (GM). Several seen on 19 January 1974, milling with Violet-green Swallows (*Tachycineta thalassina*) over irrigated fields at El Coyote (DL, SR), may have been early spring arrivals.

**Clark’s Nutcracker** (*Nucifraga columbiana*).—A clean skull and mandible found near Puerto Peñasco 16 December 1972 constitutes the second specimen (AMR) from Sonora. In autumn of 1972, nutcrackers wandered far from their usual range (even to

Piñon Jay (Gymnorhinus cyanocephalus).—Monson found 1 just across the Sonora border in Chihuahua near the top of Sierra de San Luis on 1 May 1974. Eighty foraged on the ground in mesquite grassland 6 km south of Sasabe on 11 November 1975 (GM, SR), an extension of a flight that brought many to southern New Mexico and Arizona (Witzeman, Hubbard and Kaufman, Am. Birds 30:105-110, 1976). There are no other Sonoran records.

Brown Thrasher (Toxostoma rufum).—Not listed by Miller et al. (op. cit.), but Peterson and Chalif (op. cit.) stated "casually wintering in northeast Mexico; also Sonora." It was seen at Guaymas in early December 1968 (PA). One individual at Mazatlan, Sinaloa, observed by Lamm on 12 April 1968, constitutes the only other western Mexico observation to our knowledge.

Le Conte's Thrasher (Toxostoma lecontei).—The most southerly published locality (Stephens, Auk 2:225-231, 1885) is Puerto Lobos but we have found it in small numbers south to Tepoca where it occurs in the Frankenia-Opuntia association.

Swainson's Thrush (Catharus ustulatus).—We netted 7 during the night of 17-18 September 1974 in mangroves at Punta Santa Rosa. Weights ranged from 27.0 to 34.5 g and the heavier birds had considerable subcutaneous fat. Two kept as specimens (UA) were identified as C. u. oedicus by A. R. Phillips. An intense thunderstorm a few kilometers inland produced strong winds over the coast for a short time during the night. Phillips and Amadon (op. cit.) speculated that Pacific Coast populations may migrate south just inland from the Gulf of California. These birds, presumably forced down by winds, support their hypothesis. C. m. oedicus normally "does not stop in fall north of southern Sonora" (Phillips, Marshall, Monson, The Birds of Arizona, Univ. Ariz. Press, Tucson, 1964) and the species normally migrates through the eastern foothills (van Rossem, op. cit.).

Starling (Sturnus vulgaris).—Listed by Miller et al. (op. cit.) only from Tamaulipas. In recent years it has become widespread in Sonora. Localities include Puerto Peñasco (regularly at least since 1968, RLC, GM, RW); 20 km S Nogales (first observation August 1968 ARP), El Coyote, 21 March 1974 (DL, SR); Los Hoyas, 1 March 1974 (DL, SS); and near Navojoa investigating nesting sites, 5 April 1974 (SS, DL).

Hutton's Vireo (Vireo huttoni).—The only records west of the 110th Meridian in Sonora are from Sierra Carrizal (late October 1948; Phillips and Amadon, op. cit.), Sierra del Humo (11 November, 1975, SR), and on the Sonoyta River (23 December 1968, RLC).

Prothonotary Warbler (Protonotaria citrea).—A male was seen 26 April 1972 on Río Cuchujaqui, 11 km S of Alamos (GM); the species is not previously reported from northwestern Mexico.

Virginia's Warbler (Vermivora virginiae).—The only observation of the species from a coastal area in Sonora was of 1 seen 15 April 1973, 16 km NE of El Coyote (SR).

Ovenbird (Seiurus aurocapillus).—Although the species winters regularly in Sinaloa, there has been only 1 Sonoran record, a singing male collected 21 June 1954 at Aconchi (Marshall, Pac. Coast Avif. 32, 1957). We banded single individuals in mangroves north of Chueca 21 June 1974 (wt. 16 g) and 28 May 1975 (wt. 14.6 g). The birds were not fat and had completely ossified skulls.

Hooded Warbler (Wilsonia citrina).—A male (UA) taken 30 January 1966 near Alamos in a dense thicket adjacent to the Río Cuchujaqui weighed 9.8 g. The species was not cited from western Mexico by Miller et al. (op. cit.).
Rufous-capped Warbler (*Basileuterus rufifrons*).—On 13 September 1975, Danforth et al. found a singing individual in Arroyo Cajón Bonito (Witzeman et al., op. cit.). Four singing birds were present in the same area 14 May 1976 but no mates were observed (DL, SR). The birds foraged on the north facing slope of the canyon (1280 m) in rock crevices, in oaks and junipers on the slope, and in willows and sycamores of the flood plain. Two males patrolled contiguous territories of about 2 ha, although they did not sing or approach in response to playbacks of their own songs. None was found in mid-July. The birds were about 180 km N of other localities of record (Moctezuma and moun-
tains to SE) and only 6 km S of the United States.

Great-tailed Grackle (*Quiscalus mexicanus*).—In recent years this species has ex-
tended its range virtually throughout western Sonora. It occurs along the Gulf coast at many localities as far north as Puerto Peñasco, where it has occurred regularly at least since 1965 (DL). Inland records include Sonoyta, Altar, Caborca, and Pitiquito.

Rose-breasted Grosbeak (*Pheucticus ludovicianus*).—There are no published re-
ports for northwestern Mexico. One full-plumaged male was observed 26 May 1975 8
km SSE of La Libertad (SR) and S. C. Brown collected (MVZ) an immature male 24
September 1975 near Carbo, Sonora.

Indigo Bunting (*Passerina cyanea*).—In a riparian Arizona Upland community in
Sonoran Desert scrub 65 km south of Sasabe, we noted a male singing constantly on 25
May 1975, while Varied Buntings held adjacent territories. He responded strongly to a
playback of his own song but did not react to recordings of Varied Bunting songs played
in what seemed to be his territory. The location was characterized by large flow-
ering mesquite (*Prosopis juliflora*), cat claw (*Acacia Greggii*), and huisache (*Acacia Farnes-
iana*). Sahuaros (*Cereus giganteus*) were beginning to bloom and although no grasses
or annuals were present, the vegetation present was green. On 15 July 1976 Doug Stotz
found a male singing in a riparian community dominated by mesquite and a few syc-
amoses (elev. 1250 m) near Arroyo Cajón Bonito in northeastern Sonora. Varied Bun-
tings sang nearby.

Varied Bunting (*Passerina versicolor*).—Although reported only from eastern Sonora
by Miller et al. (op. cit.), the Varied Bunting is a summer nesting species in dense
riparian communities in the Arizona Upland Subdivision of the Sonoran Desert scrub at
least as far west as Caborca. Its occurrence in a given locality in any year seems to be
dependent upon adequate precipitation. We collected (UA) a female in the mangroves
near Chueca on 22 June 1974. The bird, moderately fat and weighing 12.2 g, possessed a
partially ossified skull and an ovary less than a mm in diameter. Its worn plumage is
comparable to that of females at least 1 year old of *P. v. dickeyae*. We know of no nesting
localities in the area.

Golden-crowned Sparrow (*Zonotrichia atricapilla*).—Once recorded at Caborca (Mil-
er et al., op. cit.) and 3 seen at Puerto Peñasco 3 January 1965 (SR).

White-throated Sparrow (*Zonotrichia albicollis*).—On 2 November 1975 D. Danforth
found a single White-throated Sparrow in a dense thicket adjacent to the stream in Ar-
royo Cajón Bonito at an elevation of about 1250 m. The species occurs regularly in
southern Arizona, and this first observation in Sonora emphasizes the paucity of ob-
servers in northern Sonora.

Fox Sparrow (*Passerella iliaca*).—Cunningham observed 1 on the Sonoyta River 23
December 1968. There are no other Sonoran records.

A great number of individuals have extended their field activities to northwestern
Mexico. We are pleased to acknowledge the contributions of the many persons who
shared their observations with us. The following persons made observations which we acknowledge in the text by their initials:


We thank E. Eisenmann, G. Monson, and A. R. Phillips for reading the manuscript and offering suggestions. We also appreciate the help of R. Felger who identified some plants for us and A. R. Phillips, R. Dickerman, and A. M. Rea for identification of some bird subspecies. Permission to collect in Mexico was provided by the Dirección General de Fauna Silvestre and we are appreciative of this courtesy.—STEPHEN M. RUSSELL, Dept. of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson 85721; and DONALD W. LAMM, 6722 East Nasumpta Dr., Tucson, AZ 85715. Accepted 7 Dec. 1976.

**Egg carrying by Wood Duck.**—On 4 April 1976, we observed a hen Wood Duck (*Aix sponsa*) carrying an egg with her bill exit a Wood Duck nest box located in a beaver pond approximately 1.6 km west of Indian Mound, East Baton Rouge Parish, Louisiana. We could not determine whether the entire egg was being carried between the upper and lower mandibles or if the lower mandible was inserted into a hole in the egg. Earlier that same morning, we had seen a Wood Duck flying low over the beaver pond similarly carrying an egg-shaped object that it dropped into the water. Previously, on 2 April 1976, this nest contained 15 eggs in their 26th day of incubation. The average incubation period of Wood Ducks is 30 days (Bellrose, Ill. Nat. Hist. Surv. Circ. 45, 1953).

On the afternoon prior to the egg-carrying observation, we discovered that several eggs of this clutch had holes pecked in them. These holes may have been made by woodpeckers. Cunningham (Proc. S. E. Assoc. Game and Fish Comm. 22:145–155, 1968) has observed Red-hellied Woodpeckers (*Melanerpes carolinus*) pecking Wood Duck eggs without consuming them. He found that Common Flickers (*Colaptes auratus*) and Red-headed Woodpeckers (*Melanerpes erythrocephalus*) are also Wood Duck nest predators. All 3 woodpeckers were present at our study area. Shortly after we observed the duck removing the egg from the nest box that contained the damaged eggs, we discovered that only 7 eggs remained in the nest box. The nest was subsequently abandoned and the remaining eggs failed to hatch.

There have been previous reports of egg-carrying by waterfowl. Sowls (Prairie Ducks, Stackpole Co., Harrisburg, Pa. and Wildl. Manage. Inst., Washington, D.C., 1955:104–108) observed hen Northern Shovelers (*Anas clypeata*) and hen Pintails (*A. acuta*) carrying egg shells away from their nests that had had some of their eggs destroyed by predators. He also was able to induce an egg-carrying response by placing egg shells on top of eggs in active nests. Hochbaum (The Canvasback on a Prairie Marsh, 2nd ed., Stackpole Co., Harrisburg, Pa. and Wildl. Manage. Inst., Washington, D.C., 1959:92) witnessed a hen Northern Shoveler carrying an egg in the tip of her bill, and Lindsey (Auk 63:483–492, 1946) observed a Mexican Duck (*A. diazi*) carrying an embryo with remaining portions of a broken egg from its nest. He concluded that the egg-carrying be-
behavior he observed was a response to severe disturbance. Cunningham (op. cit.) reported watching a hen Wood Duck fly from a nest with either a whole or the greater portion of an egg in her bill. This same hen subsequently brought off a brood of 9, although 6 eggs had disappeared.

The role of egg-carrying behavior by ducks is yet unclear. However, our observations and the existing literature suggest that egg-carrying behavior is an adaptation that may increase the probability of the successful incubation of undamaged eggs in partially-destroyed clutches.—Robert W. Strader, Richard Di Giulio, and Robert B. Hamilton. School of Forestry and Wildlife Management, Louisiana State Univ., Baton Rouge 70803. Accepted 9 Dec. 1976.

Evidence of brood adoption by Ruffed Grouse.—Evidence that Ruffed Grouse (Bonasa umbellus) hens sometimes adopt chicks from other broods is scanty. Bump et al. (The Ruffed Grouse, Life History. Propagation, Management, N.Y. State Cons. Dept., Albany, 1947:293) reported a hen which had lost its clutch just before hatching that was later seen with 4 chicks. Apparent instances of 2 broods traveling together have been reported several times. Hungerford (Murrelet 34:35-40, 1953) noted a “brood” of 2 hens and 15 young. Chambers and Sharp (J. Wildl. Manage. 22:231-239, 1958) simultaneously captured 2 hens and 5 chicks of 2 age groups. On several other occasions they reported flushing groups of grouse containing young of noticeable age differences. Bump et al. (op. cit.: 293) reported occasional encounters of double broods with both hens normally present but felt that these often represented simply chance meetings of broods. They also believed that older broods may merge permanently at times, particularly if 1 hen is killed.

These reports consist primarily of chance sightings of unmarked individuals. The histories of the individuals sighted and the number of true adoptions of chicks were largely unknown. Here I present evidence that 2 radio-marked Ruffed Grouse hens adopted extra chicks in 1972 at the Cedar Creek Natural History Area 48 km north of Minneapolis, Minnesota. Brood hens were flushed at weekly intervals through early July and at irregular intervals thereafter. Chicks were counted at these times. Typically, the number of chicks seen gradually decreased as the season progressed. There were 2 exceptions. Yearling hen 2239, which hatched 9 eggs, was seen with 9 chicks 20 days after hatch and with 13 young 27 days after hatch. Three days later this hen was killed by a predator precluding additional data on her brood. Adult (22 months or older) hen 2235’s brood of 10 chicks was reduced to 4 by 30 days after hatch. However, on 4 occasions between 57 and 70 days after hatch this hen flushed with 10-15 chicks. Since home ranges of the 2 hens were adjacent. Hen 2239’s chicks conceivably could have joined hen 2235’s brood. At no time was a second adult seen with these broods.

My observations of both captive and wild Ruffed Grouse chicks indicate that by 28-35 days of age they are well-feathered, strong fliers, forage for themselves, are very adept at spotting aerial predators, and possibly could survive on their own. However, broods normally remain together about 75-85 days (Godfrey and Marshall, J. Wildl. Manage. 33: 609-620, 1969). For this behavior to be maintained by natural selection there must be a survival advantage afforded to chicks that remain with the hen for this length of time. If this is the case, orphaned or lost chicks would benefit by joining another brood.

It is more difficult to explain what evolutionary advantage a hen obtains in accepting
another hen’s chicks. Kin selection has been used to explain seemingly altruistic behavior in several species (Brown, The Evolution of Behavior, W. W. Norton and Co., Inc., New York, 1975:203). This concept seems unlikely to apply in the present circumstance since the fall dispersal pattern of Ruffed Grouse (Godfrey and Marshall, op. cit., 1969) reduces the likelihood that adopted chicks would be closely related to the hen.

Clearly, there are situations (e.g., where food is limiting) when the presence of extra chicks would be detrimental to a hen’s own young. Under these conditions a hen which adopted chicks would be selected against. Whether Ruffed Grouse hens can recognize their own chicks is not known. If brood adoption is disadvantageous, one would expect selection pressures for hens to recognize their own chicks and exclude others.

Since extra chicks apparently are tolerated, the possibility remains that hens actually benefit by accepting other chicks. After chicks are 2–5 weeks old, Ruffed Grouse eat a wide variety of plant foods (Bump et al., op. cit.: 850). Potential grouse food appeared to be abundant at Cedar Creek during this time and likely minimized the disadvantages of extra chicks in terms of competition for food. Where food is not limiting and where the effects of extra chicks in terms of predator attraction are offset by the increased probability of predator detection, a hen which adopts chicks or travels with another brood may increase her relative fitness because any chick captured by a predator would be less likely to be one of her own.

I am grateful to the personnel of the Cedar Creek Natural History Area and of the University of Minnesota Bioelectronics Laboratory (UMBL) for their cooperation during the study. I thank Richard A. Huempfner and Gary J. Erickson for assistance with the field observations. Lewis W. Oring and George-Ann Maxson made critical comments on the manuscript. This investigation was supported by the U.S. Atomic Energy Commission (COO-1332-108).—STEPHEN J. MAXSON, Dept. of Ecology and Behavioral Biology, Univ. of Minnesota, St. Paul 55101 (Present address: Dept. of Biology, Univ. of North Dakota, Grand Forks 58202). Accepted 7 Dec. 1976.

Marsh Hawks follow hunting red fox.—At 11:00 on 11 January 1973, we observed a red fox (*Vulpes fulva*) hunting among scattered clumps of dead herbaceous vegetation in an otherwise heavily grazed pasture in northern Delaware County, Ohio. Snow cover was not present. Although the fox had a severe case of mange, the animal’s behavior appeared normal. Its hunting behavior consisted of the typical canine search, pause, and pounce sequence. Two Marsh Hawks (*Circus cyaneus*) were near; 1 hawk circled at a low level over the hunting fox while the second bird perched on the ground at approximately 9 m to one side of the fox. As the fox completed its hunting activities in one clump of vegetation and moved to the next clump, 1 Marsh Hawk again perched on the ground near the fox while the other bird circled overhead. When the fox had exhausted the remaining huntable clumps in the general area and had proceeded off across the pasture, the hawks again followed. The trio was then lost from view as the fox entered an area of scattered woods at the end of the pasture. During the entire observation period of approximately 15 min, prey was not taken by either predator.

Two hypotheses may be advanced to account for the behavior of the Marsh Hawks: (1) the 2 hawks and the fox were involved in some form of cooperative feeding interaction, and (2) the movement of a small- to medium-sized mammalian predator may naturally elicit a following response among Marsh Hawks.
Cooperative feeding interactions involving two or more avian predators have been described for a number of species (Christman, Condor 59:343, 1957; Parks and Bressler, Auk 80:198, 1963; Meyreriecks and Nellis, Wilson Bull. 79:236, 1967; Dusi, Auk 85:129, 1968; Emlen and Ambrose, Auk 87:164-165, 1970; Haverschmit. Wilson Bull. 82:99, 1970; Mueller et al., Auk 89:190, 1972; Anderson, Wilson Bull. 86:462, 1974); however, only one account of a cooperative feeding interaction between an avian predator and a mammalian predator is given in the literature. Welty (The Life of Birds, W. B. Saunders Co., Philadelphia, 1975:396) described a cooperative feeding interaction which involved a Rough-legged Hawk (Buteo lagopus) that fed upon rodents dislodged by a hunting Arctic fox (Alopex lagopus).

The tendency for birds to follow mammalian predators in a situation which does not involve nest site defense has been reported for several avian predator species. Berger (Auk 73:288, 1956) gave an account of a Marsh Hawk pursuing a domestic cat (Felis domestica). A pair of Mountain Choughs (Pyrrhocorax graculus) were reported by Lane (Ibis 99:116, 1957) to follow a hunting stoat (Mustela erminea). Holland (Br. Birds 67: 212-213, 1974) observed an attraction and following tendency among Long-eared Owls (Asio otus) for a dachshund (Canis familiaris). Therefore, the tendency to follow mammalian predators may exist independently of the cooperative feeding phenomenon among Marsh Hawks and other avian predators. However, the tendency also could serve as the behavioral basis for cooperative feeding between avian and mammalian predators when the opportunity arises.—LeRoy W. Bandy and Barbara Bandy, Rt. 1, Box 75, Stetson, Maine 04488. Accepted 4 March 1977.

Predation ecology of coexisting Great Horned and Barn owls.—Food habits of the Great Horned Owl (Bubo virginianus) and the Barn Owl (Tyto alba) are well studied (e.g., Wilson, Auk 55:187-197, 1938; Graber. Condor 64:473-487, 1962), but an emphasis on feeding ecology and niche segregation is fairly recent (Marti, Condor 76:45-61, 1974). This paper details some of the mechanisms facilitating coexistence of these owls during the summer at Tule Lake National Wildlife Refuge, Siskiyou County, California.

Methods.—Observations extended from 17 June to 12 July 1975. Of the 107 km² study area, about half consisted of open water; the remainder included the eastern slope of a large ridge where both owl species roosted on rock cliffs, a region of natural vegetation along the base of the ridge, and agricultural fields to the east. The onset of owl activity at 2 rock cliffs (northern and southern, 5.3 km apart) was recorded on alternate evenings. Small rodents were trapped and tethered (with brass wire wrapped at the base of the tail) on 2 dirt roads, 1 with telephone poles and 1 without, to test the importance of high perches in the hunting patterns of the owls. Identity of predators was determined either from direct observation with a night scope or observation of wing marks and footprints around the kill. Kills of questionable identity were excluded. The presence of car and observer did not constitute a new or unusual feature at either site, since parked farm equipment is common along the roads. Habitat preferences and hunting patterns were studied by driving through the area in a non-systematic pattern between 22:00 and 04:00 PDT. Twenty-six h of these observations were recorded over 17 nights.

Pellets were used to determine food habits and were collected at weekly intervals at known owl roosts. Barn and Great Horned owl pellets were separated on the basis of size, shape, firmness, and exact location of collection, as suggested by Moon (Trans. Kans. Acad. Sci. 43:457-466, 1940); those of questionable origin were discarded.
Statistical tests follow those described by Snedecor and Cochran (Statistical Methods, Iowa State Univ. Press, Ames, 1967).

Food habits.—I analyzed 250 whole pellets and numerous pellet fragments containing 1003 prey items. Great Horned Owls averaged 3.83 and Barn Owls 2.42 prey items/pellet. A significant difference existed between proportions of different prey taken by the 2 species ($\chi^2 = 13.41, df = 2, P < 0.005$), although extensive overlap was evident (Table 1).

Activity at roosting sites.—Four Great Horned Owls were resident at each of the 2 cliffs; Barn Owls numbered 25 at the southern cliff while 5 was the maximum heard at any one time at the northern cliff. Initial vocalization and initial flight from the roost were recorded as indicators of activity onset. Great Horned Owl activity onset, though somewhat variable with respect to time (Fig. 1), was not significantly different at the 2 cliffs for initial vocalization (2-tailed t-test, $t = 0.311$, $P > 0.60$) or initial flight ($t = 0.338, P > 0.60$). Barn Owl activity, however, began significantly later at the northern than at the southern cliff (Fig. 1) for initial vocalization ($t = 4.684, P < 0.001$) and for initial flight ($t = 4.845, P < 0.001$). Although data were limited, Barn Owls also appeared to return to the roost earlier than Great Horned Owls over 4 mornings of observation. Generally they had left exposed perches for more protected roosts and their vocalization level had dropped noticeably by the time Great Horned Owls arrived at the cliffs.

Roosting sites of individual owls were divided into 3 categories based on extent of exposure. Barn Owls chose less exposed roosts significantly more often than Great Horned Owls ($\chi^2 = 13.20, df = 2, P < 0.005$). Barn Owls typically roosted far back in protected crevices or in deep holes where they were invisible from the road, while Great Horned Owls perched on exposed rocks or ledges, or in large open holes.
Table 1
Prey Items Identified in Owl Pellets Collected at Known Owl Roosts Within the Study Area

<table>
<thead>
<tr>
<th>Prey species</th>
<th>Great Horned Owl</th>
<th>Barn Owl</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of items</td>
<td>Percent of total</td>
</tr>
<tr>
<td><em>Micrurus</em></td>
<td>404</td>
<td>66.7</td>
</tr>
<tr>
<td><em>Peromyscus</em></td>
<td>167</td>
<td>27.6</td>
</tr>
<tr>
<td><em>Dipodomys</em></td>
<td>7</td>
<td>1.1</td>
</tr>
<tr>
<td><em>Sylvilagus</em></td>
<td>2</td>
<td>0.3</td>
</tr>
<tr>
<td><em>Euphaus</em> cyanopephalus</td>
<td>2</td>
<td>0.3</td>
</tr>
<tr>
<td><em>Sorex</em></td>
<td>1</td>
<td>0.2</td>
</tr>
<tr>
<td><em>Tadarida brasiliensis</em></td>
<td>1</td>
<td>0.2</td>
</tr>
<tr>
<td><em>Mustela frenata</em></td>
<td>1</td>
<td>0.2</td>
</tr>
<tr>
<td>Unidentified bird</td>
<td>8</td>
<td>1.4</td>
</tr>
<tr>
<td>Unidentified small mammal</td>
<td>4</td>
<td>0.7</td>
</tr>
<tr>
<td>Insect</td>
<td>8</td>
<td>1.3</td>
</tr>
</tbody>
</table>

1 Includes 107 Great Horned Owl pellets, 143 Barn Owl pellets, and numerous pellet fragments from both species.

Direct interspecific interactions were observed only twice; these consisted of single Barn Owls harrying or diving at single Great Horned Owls at the southern cliff. Indirect interactions occurred on at least 8 occasions when either the arrival of a Great Horned Owl at one of the cliffs or the beginning of its vocalizations was accompanied by a decline or brief cessation in Barn Owl activity and vocalizations. In addition, remains of at least 4 Barn Owls were found near the southern cliff under perches used by Great Horned Owls. Thus not only competitive interactions, but also predator-prey interactions were occurring.

Hunting behavior.—Twelve kills of tethered prey were observed on the road having telephone poles; of these, 8 were by Great Horned Owls and 4 by Barn Owls. All 6 kills occurring on the road without poles were by Barn Owls. The difference between numbers of kills by the 2 species at the 2 sites was significant ($\chi^2$ corrected for continuity = 4.640, df = 1, P < 0.05), with Great Horned Owls favoring the road having telephone poles.

Great Horned Owls made extensive use of telephone poles and to a lesser extent other perches, while Barn Owls spent more time on lower perches, on the ground, or in flight (Table 2). This necessarily limited the hunting habitat used by the larger species: Great Horned Owls were never sighted in areas where perches were not present. Barn Owls showed a more uniform distribution throughout the area, although few were sighted along the road at the base of the cliffs where the majority of Great Horned Owl sightings were concentrated.

Search and attack behavior also varied between the species. Generally, Great Horned Owls moved regularly and directly from one telephone pole to the next along a road, spending from 1 to 59 min on a pole ($\bar{x} = 7.3, n = 38$). When prey was sighted, a steep downward flight was made, with the owl sometimes banking just before landing. Usually the wings were flapped briefly on landing, after which no movement was seen for a period of $\frac{1}{2}$ to 3 min until the owl took off again, flying directly up to one of the poles nearby. Great Horned Owls were most often observed hunting alone, although groups of 2 or 3 owls
Table 2

record of Barn Owls and Great Horned Owls sighted during 26 h spent driving through the study area between 22:00 and 04:00

<table>
<thead>
<tr>
<th></th>
<th>Great Horned Owl</th>
<th>Barn Owl</th>
</tr>
</thead>
<tbody>
<tr>
<td>In flight</td>
<td>1</td>
<td>13</td>
</tr>
<tr>
<td>On perches:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Telephone poles</td>
<td>30</td>
<td>2</td>
</tr>
<tr>
<td>Signposts</td>
<td>7</td>
<td>11</td>
</tr>
<tr>
<td>Ground</td>
<td>3</td>
<td>17</td>
</tr>
<tr>
<td>Other</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Total</td>
<td>44</td>
<td>48</td>
</tr>
</tbody>
</table>

1 Observations before 22:00 or after 04:00 were excluded so that owls emerging from roosts or returning in the morning would not bias data.

were twice seen moving from pole to pole together. In both cases vocalizations occurred almost continuously between members of the group.

Barn Owls hunted primarily on the wing and occasionally from low perches. Hunting flight was usually low, with a quick erratic wingbeat or, less frequently, a fast direct flap, as described by Wilson (1938). This species was most often observed flying along irrigation channels or over strips of natural vegetation on the levee paralleling the road. Sudden steep banking drops into the vegetation were common, and owls often emerged several seconds later when unsuccessful.

Discussion.—Differences in hunting methods and habitat preferences result in reduced spatial overlap, giving Barn Owls access to areas not normally used by Great Horned Owls. These differences in hunting habits are probably physically based: the smaller size and lighter wing loading of the Barn Owl may make hunting on the wing profitable in spite of the energy expenditure, while the larger Great Horned Owl with its heavier wing loading may be constrained to hunting primarily from perches (Earhart and Johnson, Condor 72:251-264, 1970; Marti 1974).

Balancing this is the interactive dominance of the Great Horned Owl and its status as a potential predator on the smaller owl. Inhibition of Barn Owl activity by Great Horned Owl arrivals at the cliffs, a lack of Barn Owl sightings where Great Horned Owl sightings were concentrated, and remains of Barn Owls found below Great Horned Owl perches all point to the importance of this interaction. The selection of protected roosting sites by Barn Owls is consistent with this, as is the delayed Barn Owl activity onset at the northern cliff where Barn Owls were much less numerous and Great Horned Owl activity was more prolonged and conspicuous.

Host records for the Striped Cuckoo from Costa Rica.—The Striped Cuckoo (Tapera naevia) is one of only 3 species of New World cuculids that exhibits obligatory brood parasitism. Accounts of its reproductive behavior and host records have been provided by Haverschmidt (J. f. Ornithol. 96:337–343, 1955; J. f. Ornithol. 102:353–359, 1951) for Surinam and by Friedmann (Ibis (13):3:532–538, 1933) for various parts of South America.

Little is known about the habits of the species north of South America, although it is common in many lowland areas of Middle America. Aside from a single instance of parasitism on the Rufous-breasted Spinetail (Synallaxis erythrothorax) in Guatemala, which was filmed by Hugh C. Land (Wetmore, Smith. Misc. Coll. 150(2) :132–136, 1968), we can find no other host record for the species north of Panamá. Wetmore (1968) found “beautiful blue” egg-shell fragments in the oviduct of a Striped Cuckoo he collected at Buenavista, Chiriquí, Panamá on 1 March 1960, but eggs of the Middle American race. T. n. excellens, otherwise appear to be undescribed.

While working near Rincón de Osa, Puntarenas Province, Costa Rica between February–April, 1971, A. W. found the Striped Cuckoo to be common in second growth adjacent to primary rain forest at elevations <20 m. On 10 April 1971 in a second growth area about 2 km W of Rincón de Osa, he found a nest of the Plain Wren (Thryothorus modestus) which contained 1 wren egg and another egg believed to be that of the Striped Cuckoo. The nest, typical for the Plain Wren, was a retort-shaped structure composed of dry stiff grass stems and grass heads and lined with a few feathers. It was placed 1 m off the ground in the vertical fork of a small thorny shrub. The nest and eggs were collected and are now in the collection of the Western Foundation of Vertebrate Zoology (WFVZ no. 58440).

Both eggs were fresh. The wren egg is white, subelliptical in shape (after Preston in Palmer. Handbook of North American birds, vol. 1, Yale Univ. Press, 1962:13), somewhat glossy, and measures 18.75 × 14.79 mm. It is essentially identical to 10 other eggs of this species from southwestern Costa Rica in the WFVZ collection. The presumed Striped Cuckoo egg is medium blue (faded from bright greenish-blue when collected), oval (Preston 1962), lacks gloss, and measures 23.43 × 16.46 mm. These details agree with the description given by Hellebrekers (Zool. Med. Ryksm. Nat. Hist. Leiden, 24: 251–252, 1942) for 50 Tapera naevia eggs from Surinam (range of measurements = 18.7–23.5 × 14.1–17.3 mm).

Three other nests of Thryothorus modestus containing 2 eggs each were found in the Rincón de Osa area between 21 March–19 April 1971, but none contained parasite eggs. We are unaware of any previous record of Tapera naevia parasitism on Thryothorus modestus, although Wetmore (1968) suggested that this wren might be a suitable host for the parasite in Panamá and described several instances of Striped Cuckoo parasitism on a congener, Thryothorus ruficollis.

At a nearby southwestern Costa Rica locality, Sierpe, a small village near sea level, 13 km S of Palmar Sur, Puntarenas Province, L. F. K. found Striped Cuckoos to be unusually common from March to November, 1970. The species was not reported from this area prior to 1966 (Wolf, Condor 68:400–401), but it is apparently increasing in abundance in southwestern Costa Rica as primary habitats are reduced to second growth by agricultural and lumbering activities.

On 31 May 1970 on the outskirts of Sierpe, L. F. K. dismantled 1 of the massive stick nests of the Pale-breasted Spinetail (Synallaxis albescens) and found that it contained 2 spinetail eggs and another egg presumed to be laid by the Striped Cuckoo. The nest, the only one of this species examined in the vicinity, was situated in a tangle of vines on
a fencepost standing in the middle of a dense Heliconia thicket. The incubating spinetail was flushed from the nest.

The spinetail eggs were dull white when collected, but acquired a distinctly greenish tinge after they were blown. They are short oval in shape (Preston 1962) and have a rough texture. They measure 19.40 × 16.01 and 18.92 × 15.90 mm. The probable Striped Cuckoo egg is identical in color and shape to the 1 collected by Williams at Rincon de Osa and measures 22.01 × 16.45 mm. The specimens are now in the WVFZ collection (no. 51515).

While this is the first record for Synallaxis albescens as a host in Middle America, it is known to be parasitized frequently by Striped Cuckoos in various parts of South America (Friedmann 1933; Haverschmidt 1955).

The parasite eggs described here are identified on the basis of circumstantial evidence, but we believe that their designation as Tapera naevia eggs is an accurate one. In color, size, and texture they agree with published descriptions of the eggs of the 2 South American races of the Striped Cuckoo, Tapera n. naevia and T. n. chochi (e.g., Hellebrekers 1942; Friedmann 1933). Since there are only slight mensural and color differences between these subspecies and the Middle American T. n. excellens, it is reasonable to expect that their respective eggs are very similar, at least in size. Striped Cuckoos were common at both Rincon de Osa and Sierpe, and they were occasionally seen perched on the fencepost that supported the spinetail nest described from the latter locality. Finally, based on our joint experience with the nesting birds of Costa Rica and an examination of the eggs of neotropical species in most major North American collections, we know of no other Middle American species that lays eggs of this description.

Our fieldwork in Costa Rica was supported by the Western Foundation of Vertebrate Zoology and Ed N. Harrison.—LLOYD F. KIFF AND ANDREW WILLIAMS, Western Foundation of Vertebrate Zoology, 1100 Glendon Avenue, Los Angeles, CA 90024. (Present address AW: P.O. Box 23, Njoro, Kenya). Accepted 10 Oct. 1977.

Ant-following birds in South American subtropical forests.—Apart from their legendary aspects, army ants (Dorylinae) have attracted the attention of ecologists because of the interactions between the ants and their associated bird followers (e.g., Willis, Living Bird 5:187–231, 1966a; Oniki, Acta Amazonica 2:59–79, 1972). Hilty (Wilson Bull. 86:480–481, 1974) has called attention to the rarity of reports of birds associated with army ants at higher elevations, and we report here on birds associated with 2 such ant swarms.

On 16 and 19 April 1973, with R. Gochfeld and M. Kleinbaum, we visited Pichindé at about 1700 m near the crest of the western Andes above Cali, Department of Valle, Colombia. The vegetation and area have been described by Trapido and San Martin (Am. J. Trop. Med. Hyg. 20:631–641, 1971). On 19 April, on the steep slope in upper subtropical forest, above a fast-rushing stream, we encountered a swarm of small black army ants (Neivamyrmex sp.). We remained with the swarm from about 08:30 to 10:00. Our attention was attracted by the calls of Crested Ant-tanagers (Habia cristata) and Lineated and Montane foliage-gleaners (Syndactyla subalaris and Anabacerthia striaticollis). We noted up to 10 of these ant-tanagers which foraged mainly between 1 and 2 m above the ground, moving along the edge of and in front of the swarm. They were noisy, giving loud nasal jay-like calls as described by Willis (Condor 68:56–71, 1966b) and were quite animated, frequently erecting or "flashling" their red crests, sometimes main-
taining them erect for several seconds. The 2 species of foliage-gleaners were represented at the swarm by 2 individuals each. The Anabacerthia foraged in more or less upright branches mainly above 2 m, while the 2 Syndactyla remained closer to the ground and called repeatedly. During our visits to Pichindé, we found the tanagers and Syndactyla only at the swarm.

The following species were also persistent attendants at the swarm: 2 or 3 Black-billed Thrushes (Turdus ignobilis); 1 female antbird (Myrmeciza spp., probably M. immaculata), seen in low vegetation within 1 m of the ground; 1 male Slaty Antwren (Myrmotherula schisticolor) seen repeatedly over the swarm; 1 male Plain Antvireo (Dysisthamnus mentalis); 1 Spotted Barbtail (Premnoplex brunnescens), foraging 1–3 m above the ground; 2 Gray-breasted Woodwrens (Henicorhina leucosticta) actively foraging among the ants; 1 Rufous-naped Greenlet (Hylophilus semibrunneus).

Additionally, several species were seen only briefly near the swarm. For example, a male Andean Cock-of-the-Rock (Rupicola peruviana) flew right into the area where the Ant-Tanagers were calling, as if attracted to the commotion. We could not watch it in the dense foliage and do not know whether it remained and fed. Several other species appeared to be associating with the bird flock, rather than benefiting from the ants. Willis (1966b op. cit.) and Oniki (Condor 73:372-374, 1971) noted that wandering bird flocks often join ant-following flocks without actually using the ants. Thus the coalescence and disintegration of flocks of different social structure, feeding in different manners and moving at different rates, may occur regularly in subtropical and tropical forests.

Hilty (op. cit.) reported 2 species of Tangara tanagers attending mid-elevation (900–1500 m) swarms in Colombia. At Pichindé we recorded 8 species of Tangara within 300 m of the swarm (some much closer), but none actually associated with it. Significantly, the only bird common to our flock and Hilty’s was the Myrmeciza, which Willis (pers. comm.) has found to be a regular ant-follower elsewhere. Willis (1956b op. cit.) gave a detailed account of the ecology and behavior of the Crested Ant-tanager, and the habitat at Pichindé seems to be characteristic. None of the 16 mixed flocks in which Willis saw H. cristata were attending ants, and S. Hilty and R. Ridgeley have seen it at Pichindé in the absence of ants. Although this appears to be the first report of H. cristata following ants, some other members of the genus do so regularly.

Of the 45 species which Willis listed in 16 flocks, 10 occurred in the flock we observed. Of these 10, the wood wren and Slaty Antwren occurred in 9 and 8 of the 16 non-ant-following flocks studied by Willis, raising the question of whether there is a consistency to mid-elevation flocks quite apart from a common attraction to ant swarms. The Golden Tanager (Tangara arthus), one of the commonest forest birds at Pichindé, was not seen near the flock, and Willis found it in only 1 of 16 flocks. Hilty (op. cit.) indicated that the small black ants he encountered in the upper Anchicaya Valley were “presumably L. [=Labidus] praedator.” The ants from Pichindé were identified as Neivamyrmex sp. by H. Topoff. Although there have been no previous reports of birds following ants of this genus, it is likely that Neivamyrmex swarms will be attended when appropriate bird species encounter them.

On 30 January 1974, at 1550 m altitude in subtropical forest above the headquarters of Parque Nacional de Rancho Grande, Aragua, Venezuela, R. Gochfeld, M. Kleinbaum and M. G. found an ant swarm attended by 4 Black-faced Antthrushes (Formicarius analis), and 1 Short-tailed Ant thrush (Chamaea campanisoma). A Strong-billed Wood creeper (Xiphocolaptes promeropirhynchus) spent about 5 min foraging on vertical trunks 2–10 m above the swarm. Unlike Pichindé, no other species appeared near the
swarm, and the 3 species attending the swarm were silent for the entire time. The ant species was not identified.

In conjunction with Hilty’s observations (op. cit.) it appears that the paucity of reports of ant-attending birds at high altitudes may reflect the relative scarcity there of Doryline ants, and that where such ants occur, one may anticipate that some bird species will attend them. It is unlikely that professional ant-followers (in the sense of Willis, Ecology 47:667-672, 1966c; Oniki and Willis, Acta Amazonica 2:127-151, 1972), could maintain themselves more than marginally at such altitudes. Willis (pers. comm.) notes that Myrmeciza immaculata is probably such a professional, but its altitudinal range is mainly below 1700 m. In view of the scarcity of raiding ants, ant-attending birds of subtropical forests should be mainly non-professional opportunistic species, offering an interesting chance to study their behavioral interactions in the absence of professionals. Very often the most interesting insights into complex ecologic situations come from observing phenomena at the extremes of a range where atypical events are likely to occur. Further investigation of birds at high altitude swarms will provide opportunities to extend observations made at low elevations.

Our field work in Colombia benefited in many ways from the kind assistance of the late Dr. F. Carlos Lehmann whose death has meant a severe loss to neotropical ornithology. Field work at Rancho Grande was made possible by Dr. Gonzalo Medina, and we very much appreciate the advice and assistance of Paul Schwartz. Robert Gochfeld and Michael Kleinbaum participated in both trips. We thank Steven Hilty, Edwin O. Willis, and Yoshika Oniki for comments on the manuscript.—MICHAEL GOCHFELD, Field Research Center, Rockefeller Univ., Millbrook, NY 12545, and GUY TUDOR, 380 Riverside Drive, NY 10025. Accepted 17 Dec. 1976.

**Fishing behavior of Black and Turkey vultures.**—Black and Turkey vultures (*Coragyps atratus* and *Cathartes aura*) are usually characterized as carrion feeders, though both species have occasionally been observed taking live prey (e.g., Bent, U.S. Natl. Mus. Bull. 167, 1937; Mueller and Berger, Auk 84:430, 1967; Gladding and Gladding, Condor 72:244-245, 1970; Bang, J. Morph. 115:153-164, 1968). While both species are known to include fish in their diet, it has usually been assumed that the fish were obtained as carrion. Bendire (U.S. Natl. Mus. Spec. Bull. 1, 1892) however collected a Turkey Vulture which had a crop gorged with “fresh” small minnows, at least suggesting the possibility that the fish were taken alive. While discussing these species, we discovered that each of us had observed vultures fishing and decided to collaborate in the presentation of our observations. Our observations include apparent fishing by Black Vultures in Virginia and Mississippi and by a Turkey Vulture in Florida.

**Virginia.**—Just before dusk on 2 January 1975, in the Radford Army Ammunition Plant, 14 km west of Blacksburg, Virginia. Prather and Conner observed Black Vultures engaged in a behavior which looked like fishing. Beneath a large roost (Prather et al., Wilson Bull. 88:667-668, 1976) on the banks of the New River, 5 vultures stood along the bank and peered into the water. Three others on fallen limbs jutting out over the river assumed positions much like that of the Green Heron (*Butorides virescens*; Bent, U.S. Natl. Mus. Bull. 191, 1950) when fishing from a perch. A continuous rain of excrement from the roosting birds above peppered the river. This may have attracted fish. From a distance of 0.5 m above the water, one of the Black Vultures suddenly pushed with its legs and dove into the river. The bird’s head and body were completely sub-
merged, though it held its wings out of the water. The vulture immediately surfaced and made its way to shore. The success of the vulture’s efforts could not be determined.

This behavior, minus the culminating immersion, was again witnessed on 4 subsequent occasions in the month that followed. The river bank beneath the roost was searched for fish remains or other sign, but none were found. However, all perches which jutted low (0.5 to 1.0 m) over the water and were greater than 8 cm in diameter were worn smooth on the top surface, presumably by perching vultures.

Mississippi.—At 09:00, on 11 May 1976, Jackson observed 19 Black Vultures standing in the water or on concrete next to the water at the spillway of Bluff Lake on Noxubee National Wildlife Refuge, Oktibbeha County, Mississippi. One of the vultures in the water was feeding on the head of a large dead fish that had apparently washed over the spillway. Others stood motionless facing upstream or across the current (Fig. 1). Occasionally one would grab at something with its beak and one foot. One vulture captured a 6-8 cm live fish in this manner. Humans frequently fish near the spillway and undesirable fish—often injured or dead—are tossed out on the bank or back into the water. Vultures previously had been seen feeding on dead fish on the bank. Injured or dead fish in the water would be a little more difficult for the vultures to obtain but might be relatively easy to catch as they washed over the spillway.

Fig. 1. Black Vultures “fishing” at a spillway, Bluff Lake, Noxubee National Wildlife Refuge, Mississippi.
Florida.—At about 17:20, on 20 May 1976, in the East Wilderness area of Fish-eating Creek Campground, Glades County, Florida, Gaby watched a Turkey Vulture from about 10 m as it landed on the sloping bank of Fish-eating Creek. The vulture walked down the bank to the creek and into the water to a depth at which the water was almost in contact with its belly feathers. Then the bird began, apparently, to search for something in the water. It made several stabs at the surface with its bill and, at the same time, spread its wings as if for balance. When it raised its head it had a wiggling fish, approximately 10 cm long, in its bill. The vulture walked back to shore where it consumed its catch. After eating the fish, the vulture reentered the water and made additional attempts at “fishing” which were not successful.

These instances, while probably not representative of typical vulture behavior, indicate a potential for using different foraging tactics. At a time when “traditional” vulture food may be becoming less available, perhaps more aggressive and more opportunistic foraging tactics will be selected for.

We wish to thank Oscar Owre and Ren Lohoefer for helpful comments on various parts of this note.—Jerome A. Jackson, Department of Zoology, Mississippi State University, Mississippi State 39762; Irvine D. Prather and Richard N. Conner, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg 24061; and Sheila Parness Gaby, Department of Biology, University of Miami, Coral Gables, FL 33124. Accepted 18 Dec. 1976.

A new hybrid warbler combination.—An unusual warbler captured in a mist net on 12 October 1967 at Nantucket, Nantucket Co., Massachusetts, was preserved as a specimen by Baird who suspected that it was a hybrid. It was a female with an incompletely ossified skull and weighed 12.0 g. On comparison with other preserved material, the bird was tentatively identified as a hybrid Yellow-rumped (Myrtle), *Dendroica coronata*, × Bay-breasted, *D. castanea*, Warbler. It was similarly and independently identified by Banks after comparison with material in the National Museum of Natural History. This hybrid combination was not mentioned by Gray (Bird Hybrids, Commonwealth Agric. Bur., Farnham Royal, Bucks, England. 1958) and has not, to our knowledge, been reported in subsequent literature. The following comparative description is based on immature (first fall) females of the presumed parental species.

The hybrid Myrtle × Bay-breasted Warbler (USNM 567882) is very similar dorsally to a Blackpoll Warbler (*D. striata*) and might easily be mistaken for that species at a glance. It is, however, slightly darker and somewhat grayer. The back and nape color is intermediate between the rather bright yellowish-green of the Bay-breast and the brownish of the Myrtle. The crown of the hybrid is lighter than the back, approaching the color of the Bay-breast. Feathers of the crown have, distal to the basal gray area, a small spot of white along the rachis and a suffusion of yellow extending onto the vanes; the tips of these feathers are green. Neither the white nor the yellow is as extensive as in the Myrtle Warbler. There is a yellowish cast on the rump feathers of the hybrid, but none of these feathers has the bright yellow tip characteristic of the Myrtle. The upper tail coverts are edged with silvery gray, as are those of the Myrtle, in contrast to the green-tipped gray coverts of the Bay-breast.

The ventral body surface is essentially plain, with a faint band of dark spots across the breast. Some of the flank feathers, particularly the more posterior ones, have dark
shaft streaks. In both of these characters, the hybrid is similar to the Myrtle, although not as extensively marked. The abdomen is white as in the Myrtle. Otherwise the ventral coloration (including the under tail coverts) is buffy as in the Bay-breast, although paler. This buffiness rules out D. striata as a possible parent. There is a very slight yellowish cast on some mid-flank feathers but no indication of yellow on the throat. There are large white spots on the inner vanes of the outer 2 rectrices on either side, and a smaller white spot on the third rectrix on the right. The Bay-breasted Warbler typically has such spots on the outer 2 rectrices, the Myrtle on the outer 2 or 3. The small amount of white on the rectrices and the lack of yellow on the throat, as well as consideration of geographic ranges, eliminates the Audubon type of Yellow-rumped Warbler from consideration as a possible parent.

Measurements (by Banks) of a small series of each parental form indicate that although there is considerable overlap, the Myrtle Warbler averages slightly smaller than the Bay-breast in wing and tarsus length and the Bay-breast is slightly smaller in length of the tail and middle toe. In each of these measurements, the hybrid is smaller than the mean of the smaller species, although within the range of variation of the smaller or of both parental forms. There is little overlap in the length of the bill, measured from the anterior edge of the nostril, in the parental species, the Bay-breast being longer billed. The presumed hybrid is very near the mean of the Myrtle Warbler in this measurement. Thus the hybrid is in most respects smaller than either parental species, in contrast to the intermediate size often noted in hybrids.

Parkes (Condor 63:348-449, 1961) has pointed out that all known wood warbler hybrids are either intergeneric or between members of closely related species-pairs. This seems to be the first report of an intrageneric hybrid between species not members of a species-pair.

In characterizing the genus Dendroica, Ridgway (U.S. Natl. Mus. Bull. 50, pt. 2, 1902) noted that the wing is rather pointed with the “four outermost primaries abruptly longest . . .” except in the distinctive rounded-winged Antillean species and in D. magnolia, in which the outer primary is reduced. He did not mention that in 3 species—D. castanea, D. striata, and D. caerulea—only the 3 outermost primaries are abruptly longer than the inner ones (D. fusca nearly approaches this condition). The hybrid is similar to D. coronata in having a wing tip made up of 4 long feathers rather than 3 as in D. castanea.—RICHARD C. BANKS, Div. of Cooperative Research, U.S. Fish and Wildlife Service, Washington, D.C. 20240, and JAMES BAIRD, Massachusetts Audubon Society, Lincoln, MA 01773. Accepted 26 Sept. 1976.
ORNITHOLOGICAL LITERATURE

SEXUAL SIZE DIMORPHISM IN HAWKS AND OWLS OF NORTH AMERICA. By Noel F. R. Snyder and James W. Wiley. Ornithological Monographs No. 20, 1976:vi + 95 pp. American Ornithologists' Union. $7.50.—The chief original contributions of this paper are (1) a table summarizing food habits of all species of hawks and owls in North America for which significant data are available in Fish and Wildlife Service files or published literature; (2) a table of dimorphism indices and the mean measurements of wing chord, culmen, and weight on which these indices are based; (3) extensive data on food, feeding rates and timing of reproductive losses at nests of the Sharp-shinned Hawk (both Puerto Rican and mainland subspecies), Cooper's Hawk, Goshawk, and Red-shouldered Hawk; (4) excellent new data demonstrating substantial sexual differences in diet in Sharp-shinned and Cooper's hawks; and (5) 4 bivariate scatter diagrams that individually relate average dimorphism in both hawks and owls to % birds ($r_s = .79$), % mammals ($r_s = .06$), % lower vertebrates ($r_s = .16$), and % vertebrates ($r_s = .43$) in the diet. The correlation of dimorphism with % birds is highly significant; that with % vertebrates is weakly significant, resulting mainly from the inclusion of the component of avian prey. From this the authors conclude (p. 9) that “The correlation between size dimorphism and taking of avian prey is sufficiently strong that we consider it to be the most important fact to be handled by any hypothesis concerning the function of size dimorphism in raptorial birds.”

On the basis of these findings, Snyder and Wiley present a novel refinement of existing theory that relates sexual size dimorphism to adaptively-broadened intraspecific niches. Specifically, they propose that substantial dimorphism in bird-feeding raptors has been selected for because it reduces intra-pair competition and allows a wider range of food sizes to be taken during the crucial period late in the breeding cycle when both sexes are foraging and when such predators are food stressed because of reduced bird populations. Young of these birds of prey, requiring extended practice to develop the expertise necessary to capture birds, may be especially vulnerable to food shortage during their prolonged post-fledging dependency period.

Although the authors achieve only moderate success in supporting their argument with field data, especially those obtained from nesting accipiters, even when their efforts lead to rather equivocal results one gains the impression that they are seeking answers in the correct places. It is unfortunate that the general paucity of published information on feeding ecology of hawks and owls late in the breeding season renders their hypothesis difficult to test with information from other species. Nonetheless, Snyder and Wiley’s stimulating thoughts on dimorphism deserve continuing consideration as new information accumulates.

In addition to a thorough review of ideas proposed in the past for the sexual size difference in raptors, they also discuss the related question of why the female is usually the larger sex. After briefly entertaining the notion that reversed dimorphism “is possibly a chance effect,” they conclude, in at least partial agreement with Amadon (Raptor Research 9:1-11, 1975), that the reversed nature of the dimorphism is likely to be “related to advantages in copulation, incubation, brooding, and nest defense for large females.”

The most impressive aspect of this monograph is the thoroughness and balance of the discussion, which interweaves both old and new explanations for dimorphism in a most satisfying way. The many alternative views already in the literature are weighed fairly, with no apparent urge to seduce the reader into following poorly-illuminated paths. In
Table 1

Relationship Between Size Dimorphism and % Birds in Diet in North American Hawks and Owls

<table>
<thead>
<tr>
<th>Taxa included</th>
<th>Type of dimorphism index</th>
<th>Number of species</th>
<th>$r_s$</th>
<th>Statistical significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawks and owls</td>
<td>Average$^2$</td>
<td>44</td>
<td>0.79</td>
<td>$P &lt; 0.001$</td>
</tr>
<tr>
<td>Owls</td>
<td>Average</td>
<td>17</td>
<td>0.71</td>
<td>$P = 0.001$</td>
</tr>
<tr>
<td>Hawks</td>
<td>Average</td>
<td>27</td>
<td>0.85</td>
<td>$P &lt; 0.001$</td>
</tr>
<tr>
<td>Hawks below D. I. of 7.5</td>
<td>Average</td>
<td>13</td>
<td>0.13</td>
<td>$P &gt; 0.100$</td>
</tr>
<tr>
<td>Hawks above D. I. of 7.5</td>
<td>Average</td>
<td>14</td>
<td>0.71</td>
<td>$P = 0.010$</td>
</tr>
<tr>
<td>Hawks and Owls</td>
<td>Body weight$^a$</td>
<td>35</td>
<td>0.93</td>
<td>$P &lt; 0.001$</td>
</tr>
<tr>
<td>Owls</td>
<td>Body weight$^a$</td>
<td>16</td>
<td>0.54</td>
<td>$0.01 &lt; P &lt; 0.025$</td>
</tr>
<tr>
<td>Hawks</td>
<td>Body weight$^a$</td>
<td>19</td>
<td>0.81</td>
<td>$P &lt; 0.001$</td>
</tr>
<tr>
<td>Hawks below D. I. of 8.1</td>
<td>Body weight</td>
<td>9</td>
<td>0.09</td>
<td>$P &gt; 0.100$</td>
</tr>
<tr>
<td>Hawks above D. I. of 8.1</td>
<td>Body weight</td>
<td>10</td>
<td>0.36</td>
<td>$P &gt; 0.100$</td>
</tr>
</tbody>
</table>

$^1$Based on analysis, with the Spearman Rank Correlation Test, of data from Table 1 of Snyder and Wiley.

$^2$“Average Dimorphism Index” of Snyder and Wiley is computed as the mean of separate indices calculated for wing chord, culmen, and body weight.

$^a$Based on cube roots of mean weights of males and females.

In addition to discussion of the possible dimorphism-food relationship, the paper is replete with ad hoc hypotheses involving other ecologic features and their possible relevance to the size difference between the sexes. Thus, correlations are attempted between degree of size dimorphism and incidence of double-brooding, degree of coloniality, polygyny, and sex ratio in various raptorial species, including those that do not fit neatly into the apparent relationship of degree of dimorphism and percent avian prey. To be sure, many of these comparisons do not yield convincing correlations, suggesting that the explanation underlying the evolution of dimorphism could be more complicated than researchers in this area have admitted. If the selective pressures that influence dimorphism vary among species, through time, and by geographic region, as could well be the case, then the data necessary to expose the real biologic correlates of sexual size difference will need to be correspondingly refined and extensive. Those who interpret this conclusion as an unnecessary retreat into complexity are reminded that it also could represent an advance into reality. Simple answers are unlikely to questions that have puzzled naturalists for over a century.

Because the authors do not separately analyze the various groups of raptors included in their biologically important and statistically significant plotting of % birds in diet against average dimorphism (Fig. 1, p. 7), I have taken the liberty to examine their data in this light. The results of my comparisons are presented in Table 1. Of immediate interest is that owls follow the same trend as hawks even though they do not reach the striking indices of dimorphism shown by the latter group. Inspection of Snyder and Wiley’s plotting of the hawks alone exposes yet another area of concern. Below an average dimorphism index of approximately 7.5, only species that feed to a minor extent on birds are represented and no correlation of sexual size difference with the taking of avian prey is seen ($r_s = 0.13$). Above an average dimorphism index of 7.5, however, strong correlation is demonstrated. Thus, a gradual increase of dimorphism with increasing avian
feeding is not seen in approximately one-half the species of hawks. But when dimorphism reaches a certain (threshold?) level, the sexual size difference is dramatically correlated with percent birds in the diet. Most impressive of all is that the highest levels of dimorphism in owls occur in the same region of the scale where the hawks shift from non-correlation to correlation with avian diet. Comparison of these trends in dimorphism with those of birds of prey of other geographic regions should be most rewarding. Space does not permit speculation here on the reasons for these patterns in North American species.

In the opinion of many, body weight is far superior to other measurements as an assessment of overall size. Thus, I was disappointed to note that Snyder and Wiley base all their size comparisons on an average dimorphism index calculated as the mean of 3 separate indices, those of wing chord, culmen, and weight. For many species the indices are rather similar and nothing would appear to be gained by using the body weight index. But for others the difference is dramatic and an index obtained by averaging simply conceals the true magnitude of the size difference between the sexes. For example, in the Great Gray Owl the index based on weight is 10.9, versus 6.3 for the average index. Comparable figures for the Short-eared Owl are 6.1 versus 2.5. Therefore, comparisons of dimorphism indices based on body weight with % avian food are of interest, and I present these data in the bottom half of Table 1. In general, the findings compare favorably with those derived from the average index. The combined groups of birds of prey show a substantially higher correlation than when the average index was used. Independent comparisons of owls and of hawks again provide statistically significant Spearman correlation coefficients. Once more a break is evident in a plotting of the hawks, in the vicinity of dimorphism index 8 and between 10 and 20% birds on the scale. Surprisingly, when the 2 groups on each side of the shift are analyzed separately, neither correlation is statistically significant. Although the reasons for this are not clear, I suggest that in hawks, the dimorphism index based on weight correlates well with % of birds taken as food, mainly because the means of 2 rather independent groups are correlated. Within either group, however, the scatter is substantial and no significant correlations are evident. Thus, there are still many puzzling aspects of the relationship between degree of dimorphism and diet in addition to those illuminated by the authors.

In conclusion, my overall impression of this monograph is very favorable. Snyder and Wiley are to be commended for enlivening the rather static theoretical framework upon which discussions of sexual dimorphism have rested in recent years. Whether arguments supported principally by data from accipiters will deserve generality depends upon information yet to be gathered from other species already studied superficially as well as from additional birds of prey inhabiting geographic regions beyond North America. Hopefully many of their suggestions and tangential leads will be followed by the current army of raptor enthusiasts now alerted to this fertile ground.—Ned K. Johnson.

Ornithological Gazetteer of Paraguay. By Raymond A. Paynter, Jr., and Alastair M. G. Caperton. Museum of Comparative Zoology, Cambridge, Mass., and Field Museum of Natural History, Chicago, Ill., 1977: iv + 43 pp., 2 maps. paperbound. $1.75. Order from Bird Dept., Mus. Comp. Zool., Harvard Univ., Cambridge, Mass. 02138 or Bird Division, Field Mus. Nat. Hist., Chicago, Ill. 60605.—This is the third, and much the smallest, of the useful series of gazetteers of Neotropical localities where birds have been collected or observed. Melvin A. Traylor, Jr., the coauthor of the volumes on Bolivia
and Ecuador, continues (with Paynter) to edit the series, but the present volume's authorship changes to Paynter and Caperton; the latter is credited in the editors' introduction with having prepared the preliminary draft. The general format remains the same as in the earlier volumes. The outline map (printed on the back cover as well as on p. 43) reflects recent changes in the boundaries of the departments of Paraguay, which in some instances are quite different from those shown in standard atlases such as that published by The Times of London. The map on p. 36 pinpointing collecting localities shows the astoundingly small area of Paraguay from which birds have been obtained. Most of the localities lie along the major rivers, except for a belt across the Chaco and a scattering in the north and central portions of the area between the ríos Paraguay and Paraná, in the eastern half of the country. The northern half of the Gran Chaco, perhaps one-third of Paraguay, remains ornithologically unexplored; it is hardly surprising that most of the collecting localities of the newly discovered third species of living peccary, *Catagonus wagleri* (Wetzel, Bull. Carnegie Mus. Nat. Hist. 3, 1977), lie within this little-known region.

As in the case of the gazetteer for Ecuador, the authors have attempted a complete bibliography. At least one major paper was omitted: "Catálogo sistemático de las aves del Paraguay," by B. Podtiaguín (Rev. Soc. Cient. del Paraguay 5 (5), 1941), which includes a detailed review of Cuculidae and the description of a new subspecies, *Crotophaga ani lapchinskyi* (p. 90) from Villa Hayes: Río Verde, kl. 4, Chaco. In the first 20 pages of this paper are listed at least 9 localities that are not in Paynter and Caperton's gazetteer (Bernal-cué, Camacho, Colonia Elisa, Colonia Santa Lázara, Estancia Suhin, Fortín Page, Puerto Juan Barbero, Río Confuso, and San Ignacio).

As I stated in my review of the Ecuador gazetteer (Wilson Bull. 89:638–639, 1977), I see no reason for haste in preparing these publications, which should be as nearly definitive as possible when issued. The editors continue to deny themselves the assistance available from colleagues working on Neotropical ornithology, by their failure to circulate the manuscripts of their gazetteers in advance of publication.—KENNETH C. PARKES.

**The Wrens.** Record # ARA-2. Produced and narrated by John William Hardy. Principal recordist, Ben B. Coffey, Jr. Produced in the Bioacoustic Laboratory of the Florida State Museum. Published privately by John William and Carol K. Hardy, Gainesville, Florida, 1977. One LP record in jacket. $6.00.—This is Hardy's second record, and it is a notable success. As with his first record (reviewed by me in Wilson Bulletin 88:525–526) his objective is not only to provide listening pleasure but also to educate the listener. In this one there is rather more emphasis on pleasure and less on education, but the same format is used. Written information is confined to the back of the jacket, while a considerable amount of spoken information accompanies each recording. Forty-three of the 60 wren species are presented—a worthy achievement in itself—and in most cases there are several cuts for each species, often from different localities. These are listed on the jacket, together with the bare details of the recording. The rest of the jacket contains a general introduction to the family, a discussion of wren vocalizations, brief taxonomic comments, and a list of species not on the record. In the spoken commentaries there is no standard species treatment (nor need there be); Hardy merely highlights the most interesting points about each recording. Range and habitat, and sometimes plumage notes, are given for each species, but most of the comments concern the vocalizations. Topics discussed include song type (solo/duet), function,
geographic variation, and taxonomic relationships, with a frequent nod to aesthetics. For Hardy the wrens are “perhaps the ultimate songbird family,” and the record goes far toward proving him right. He believes that wren voices “may be the evolutionary counterpart in voice to the birds of paradise or the hummingbirds.” It is clear that he is completely charmed by wren voices—but so is everyone who has birded in the neotropics, myself included. None who listen to this record can doubt that the wrens are among the world’s greatest songsters. Hardy’s original objective was to display some of the “stunners” in the family, but as an ornithologist he was also concerned to “survey as much of the family as possible, to give scientists food for thought about systematic relationships and ecological aspects of bird voice.” He succeeds in all these objectives.

Most of the recordings are of the highest quality. Some less good ones are included, either to illustrate some point or because they are the only recordings of a particular species, and this is as it should be since the author is trying to inform as well as entertain. This record marks the emergence of Ben B. Coffey, Jr. as a top-notch field recordist. Two-thirds of the recordings are his, and they are uniformly superb. He traveled far and wide to obtain them, and is to be congratulated on a fine achievement. This is not to imply that the other recordists have not also made noteworthy contributions—credit is due to John Arvin, Luis Baptista, Richard Bradley, John Fitzpatrick, Michael Gochfeld, William Gunn, Charles Hartshorne, P. P. Kellogg, David Lee, Ted Parker, and Paul Schwartz, while Hardy himself contributed one of the recordings.

The jacket cover features a simple but charming black-and-white drawing by Richard Bradley of 2 wrens, together with sonograms of their voices.

No production is without defects, and the principal one here concerns the spoken commentary, which is much too long. The same problem marred Hardy’s first record, where there was almost more commentary than bird song. Here he has cut back the human voice somewhat, but not nearly enough. It is not without reason that nearly all bird records present the commentary in written form, either on the jacket or in an accompanying booklet. The human voice pall on repetition while bird songs do not; the space taken up by the human voice can be used for more bird songs; and information retrieval from a spoken commentary is extremely difficult. To find out what Hardy says about a given species you either have to play through the whole side (the material is not divided into bands as in many records) or take a stab (literally) at finding the right spot by dropping the needle on the record. Your record will likely soon be covered with scratches. Hardy is aware of these objections, yet defiantly presses his maverick approach. Hear him you will, whether you like it or not. He suggests that anyone who gets tired of the commentary can make a tape copy of just the birds, to which I can only reply, “Thanks a lot!”

Hardy says it is possible that Coffey’s recording of Cistothorus platensis from Colombia may in fact be C. apolinari, whose voice was not known at the time, but I can confirm that it is in fact platensis. A similar recording made by Michael Gochfeld near Bogota turned out to be C. platensis tamae, whereas C. apolinari, which we both recorded elsewhere, has a totally different voice.

The jacket is not without faults. Sloppy typesetting in the genera Odontorchilus and Hylorchilus has resulted in duplication and confusion. Timberline and Mountain wrens are nos. 34 and 33 on the jacket, but on the record the Mountain Wren comes first. And where are the curious Colombian localities “Above and W. Uribe” listed for Thryothorus genibarbis? I found Uribe in my atlas; perhaps W. Uribe is a western suburb. I could not find Above (Abové?); but then, some Colombian villages are very small.
In spite of some drawbacks this is an important record. A lot of voices are here published for the first time; Hardy provides much good information; and above all, the songs of the wrens are sheer delight. For anyone interested in bird voices, this record is a "must."—STUART KEITH.

VERTEBRATES OF FLORIDA. By Henry M. Stevenson. University Presses of Florida, Gainesville, 1976:607 pp., 11 plates, 15 figures, 68 maps. $35.00.—The subtitle, identification and distribution, points out the author's objectives, namely to provide in one book the means to identify specimens of all the land and freshwater vertebrates known to occur in Florida, and to outline their distributions. The book is organized into 4 chapters; an introduction, the keys, the species accounts, and descriptions of techniques for collecting and preserving vertebrates. A glossary, which is subdivided into sections on fishes, herptiles, birds, and mammals, and an 18 page bibliography, which includes references to the first occurrences in Florida of many vertebrates, are useful. The illustrations, though functional, are uniformly unesthetic. In all, 880 species are included. The author has done well at keeping the contents updated. He treats numerous exotics that have established feral populations recently, and the many accidentals that have been recorded in recent years.

In addition to students, teachers, and amateur naturalists, the ever-growing group of environmentalists will find the book useful. Unfortunately its price will prove too high for many. I have tested the keys with a few specimens from all 7 classes. Based on this admittedly insufficient sample, the results are good. To reach the proper species, one must first correctly establish the class, order, and family. I like this requirement because it reinforces knowledge of vertebrate classification. Keying birds requires total length measurements. In the introduction the author defends using this approach, although he has failed to convince several colleagues, including me.—GLEN E. WOOLFENDEN.

WILDFOWL OF EUROPE. By Myrfyn Owen, illus. by Hilary Burn and Joe Blossom. Macmillan London Ltd., 1977:256 pp., 55 color plates, many line drawings and maps. £12.00. —This is an authoritative but nontechnical review of the ducks, geese, and swans of Europe. The author, Conservation Research Officer for the Wildfowl Trust at Slimbridge, England, has combined a concise but smoothly written text with an unusually fine collection of illustrations to produce a work that should please both the reader's scientific and esthetic appetites. The first quarter of the book is devoted to 7 chapters dealing with general aspects of waterfowl biology, including relationships, environment, population structure, banding studies and migration, behavior, and relations with humanity. The bulk of the work, however, is concerned with individual accounts of the 55 European species. Each account covers identification, voice, breeding behavior, distribution, feeding habits, and other subjects of interest. Appendices summarize information on nests, eggs, and young; winter weights and measurements; winter foods; and breeding records and special requirements of birds in captivity. Much of this information is from previously unpublished records.

There are 55 full page color plates painted by Hilary Burn. These illustrate the various species in natural poses, showing sex, age, and seasonal plumage differences, as well as downy young. These paintings are extremely lifelike and attractive. There are also many
skillful line drawings by Joe Blossom, and a full set of range maps. The book includes a foreword by Peter Scott and a bibliography.

Wildfowl of Europe is a handsome addition to the extensive illustrated literature of this most popular group of birds.—Robert J. Raikow.

ONTOGONY AND PHYLOGENY. By Stephen Jay Gould. The Belknap Press of Harvard University Press, Cambridge, Mass., 1977: 501 pp. $18.50. — Generations of students have learned that "ontogeny recapitulates phylogeny." The tenacity of this concept arises not only from the axiomatic finality of the statement, but also because there is clearly some kind of relationship between the stages of embryonic development and the patterns of similarity between organisms. In this book Stephen Jay Gould reexamines the relationships between ontogeny and phylogeny and attempts to provide a new assessment of their significance. For the most part he succeeds admirably, though the complexity of the result precludes any simplistic summary slogan comparable to Haeckel's pithy aphorism. The first part of the book reviews the history of ideas about ontogeny and phylogeny, while in the second a somewhat eclectic, but basically new theory is developed.

From Aristotle to the Naturphilosophen of the late 18th and early 19th centuries various analogies were drawn between the stages of ontogeny and some scale of organic perfection. Aristotle saw in human development the successive levels of nutritive (corresponding to plants), sensitive (animal) and rational (human) beings. Later philosophers developed detailed scales of being from lower to higher forms. Although they form a background to the recapitulation theory, these concepts were mostly idealistic rather than evolutionary. The great 19th century embryologist Karl Ernst von Baer is often regarded as a supporter of recapitulation, an idea encouraged by Haeckel, but Gould makes clear than von Baer actually opposed Haeckel, and argued that development is a process of differentiation rather than recapitulation.

With the advent of evolutionary theory, recapitulationists developed a model in which animals evolved by adding new stages to the ends of unchanged ancestral ontogenies. At the same time these ontogenies became condensed in duration so that successive terminal additions became telescoped backward into shortened earlier stages. Thus the series of ontogenetic stages was considered to be a condensation of successive ancestral adult stages. Ernst Haeckel codified this theory as the Biogenetic Law. He recognized that developmental features could be modified out of sequence, but accommodated these exceptions as merely inconvenient falsifications of the true history.

In a fascinating digression Gould reviews the profound effect that Haeckel's theory had on such diverse areas as criminal anthropology, racism, theories of child development, and Freudian psychoanalysis.

Early in this century the recapitulation theory was gradually discarded not through disproof (it accommodated all exceptions) but because embryologists turned from a search for ancestors to a search for the causal mechanisms of development, for which the theory was irrelevant. Mendelian genetics showed that the determinants of heredity could act not just terminally but at all stages of development, and that genes often act by controlling the rates of processes. Recapitulation was abandoned as a universal principle in favor of a general model in which it was only one of several modes of evolutionary change resulting from shifts in the timing of developmental events.
In *Embryos and Ancestors* (originally published as *Embryology and Evolution*) Gavin de Beer described 8 categories of *Heterochrony*, or evolutionary changes in the timing of developmental events. Gould argues that 4 of these involve the introduction of new characters rather than changes in timing, but that 4 others are true examples of heterochrony. Reorganizing de Beer's ideas he presents a new theory of heterochrony distinguishing between developmental *processes* and their morphological *results*. The processes are (1) *Acceleration*: the development of a feature is shifted to an earlier stage in ontogeny, and (2) *Retardation*: a displacement to a later stage compared to ancestral ontogenies. There are also 2 possible results. (1) *Recapitulation* is the repetition of ancestral adult stages in the descendent’s embryonic or juvenile phase. It may arise either by the acceleration of a feature, or by prolongation of the life history. (2) *Paedomorphosis* is the retention of ancestral juvenile characteristics by later developmental stages of descendents. There are 2 distinct types of paedomorphosis. *Progenesis* results from the precocious sexual maturation of a form with otherwise juvenile morphology (often including small size). *Neoteny* results from the retardation of somatic development, though body size may equal or exceed that of ancestral forms. Examples of progenesis are drawn from various invertebrates; neotenic vertebrates include some urodeles, humans, and ratite birds. Gould, like many previous authors, redefines various terms. This source of possible confusion is clarified by an excellent glossary in which many terms are not only defined, but changes in their meaning are traced.

A unique aspect of Gould's theory is the attempt to tie reproductive strategies to environmental conditions. He suggests that paedogenesis allows adaptation to different sets of environmental constraints on population growth. Progenesis is an adaptive response to r-selective regimes, and neoteny to K-selection. Under conditions where population size is not density restricted, r-selection predominates. Where populations lie well below the carrying capacity of the environment, selection will favor strategies that maximize growth, at least until the carrying capacity is reached. Such populations tend to fluctuate widely in response to frequently unpredictable variations in the environment. Progenesis is effective here because early maturation and rapid development favor rapid population increase. K-selection operates in more stable environments to maintain relatively constant populations at or near the carrying capacity of the environment. K-selected organisms typically produce few young, but these have a relatively high probability of survival to reproductive age. Populations are density limited, and there is strong selection pressure for individual success. The argument is developed by Gould mainly in terms of human evolution. Humans are shown to be neotenic, with attendant long gestation and dependency periods.

The main problem here is that the validity of Gould's thesis ultimately depends on the validity of the existing theory of r and K selection. Though widely used as a pedagogic model, the theory embodies many difficulties and may be too simplistic to have the generality that Gould requires. The question was recently reviewed by Stephen C. Stearns (Ann. Rev. Ecol. Syst. 8:145–71, 1977) who concluded that we still lack a general and reliable theory of life history evolution.

Finally, Gould makes brief mention of recent biochemical studies showing that humans and chimpanzees are nearly identical in structural genes, and that their profound organismal differences must be due mainly to changes in genetic regulatory mechanisms. He concludes that these proposed changes are heterochronic in nature.

Although this book contains few specifically ornithological references, its provocative ideas should be of interest to all workers concerned with the evolution and ecological relationships of birds.—Robert J. Raikow.
OPTICAL SIGNALS: ANIMAL COMMUNICATION AND LIGHT. By Jack P. Hailman. Indiana University Press, Bloomington, Ind., 1977: 362 pp. $15.00.—A theoretical analysis of visual communication in animals, including both markings and movements. Although there are many examples dealing with birds, the emphasis is on the nature of the process of communication rather than on any particular group of animals.—R.J.R.

NORTH AMERICAN BIRD SONGS: A WORLD OF MUSIC. By Poul Bondesen. Scandinavian Science Press Ltd., 2930 Klampenborg, Denmark, 1977: 254 pp., over 225 sound spectrograms. $15.50.—This book has some outstanding merits, some features difficult to evaluate, and some minor defects. The defects are to be expected, considering the complexity and difficulty of the task the author set himself, which was to make a detailed study of one large geographical segment of the world of bird music—a segment distant from his own country—and to employ a language other than his own in expressing his results. The courage and ability shown in this undertaking justify a certain patience on the part of the reader. This is the more true as the task is unprecedented. A. A. Saunders (the incomparable) did something like it for the Eastern U.S., but before the days of sound spectrograms. A. V. Arlton, in his Songs and Other Sounds of Birds (lithographed only), put the vocalizations of 170 species into musical notation with some verbal description and analysis, but most ornithologists are unable to profit from musical notations for songs.

The 290 species dealt with in this book are a large part of the passerine birds in the continental U.S. and Canada, but do not include any nearctic species found exclusively South of the Mexican border. The spectrograms are each given more page space than those in Birds of North America by Chandler Robbins et al., but they are mostly made with a wide-band machine and hence, while giving admirable temporal resolution, are often less helpful as to frequency than the tiny ones in the other book. One feels this especially with clear-toned species, e.g., chickadees, Bachman’s Sparrow, or Hermit Thrush. I prefer the narrow-band filter, but the ideal (apart from expense) would be to use both for each species.

The introductory essays on analyzing, describing, and reproducing songs and on song behavior are helpful. There is a list of gramophone records, an index (of birds only), a good glossary or “vocabulary,” a short but well chosen bibliography, and 439 items of literature cited. In addition to his own careful analyses of songs, Bondesen quotes freely from other authors. This helps to make the book a useful reference work. The verbal descriptions and spectrograms admirably supplement one another.

Certain unidiomatic phrases and eccentric word usages may give readers trouble. Here are perhaps the most serious: staccato (p. 233) for “short or long figures having an almost constant frequency” (italics added); monotone (pp. 17, 42), for monotonous repetition of “figures, motifs, or phrases” (which may internally have wide frequency contrasts); phrase (pp. 40, 70, 232) for what some writers call a song; continuous (p. 41) for a sound sequence “not consistently divided into phrases” (rather than for the absence of substantial pauses between successive utterances). The above 4 words are crucial for the author’s purposes, but only staccato and phrase are defined in the vocabulary. I emphatically agree with the hint that “exclusion,” or the omission, now and then, of a part of a bird’s song-pattern or phrase contributes to variety, the achievement of contrast.

Features not easily evaluated are: the classification or “key” for songs—rather different from the one Saunders provided—which Bondesen offers as an aid to identification; also the arrangement of species in an order determined by the key rather than in a standard taxonomic sequence. Thus Bachman’s Sparrow and the Blue-winged Warbler
appear on the same page. The intricate and ingenious key is not easy to grasp, and opinions as to its usefulness may differ. Singers are divided into 3 basic groups: I, II, and III, or the Starling, Warbler, and Thrush groups. Some species have songs falling into more than one group. More than two-thirds are put into Group II, which might also be termed the Warbler-Finch group, since besides parulids, it includes most of our fringillids. Group III includes turdids, mimids, vireos, and a few fringillids. The groups are divided and subdivided by various criteria.

Starling-type songs (30 spp.) are largely formless, lacking in "architectonic structure." Both Warbler and Thrush songs are more or less structured and well-patterned. Warblers and many finches sing their phrases with monotonous repetition ("bound composition") and (at least in Group III) with long pauses, compared to the Thrushlike singers, with their nonmonotonous or "free" composition and short pauses or none. These facts, as the author seems to hint (p. 17), conform at least partially to my thesis that birds tend to avoid repetition relieved by pauses.

Bondesen refers to Dobson and Lemon (Nature, 257:26-28, 1975) who critically discuss this "antimonotony" rule. The discussion helps to clarify the issue. Biological or behavioral generalizations usually require qualifications; some of these are (though inadequately) stated in my book, Born to Sing, which the author lists. What I meant by the "monotony threshold" was not a positive correlation of overall versatility (size of repertoire) with continuity of singing (high ratio of song or phrase lengths to length of pauses), but rather a negative correlation between singing repetitively, or without "immediate variety" (changes of tune not after minutes but after at most a few seconds) and the absolute length of pauses between phrases. Monotony, for fast-living singing animals, is avoided either by changing the music or by pauses long enough for memory to fade. With this understanding both Bondesen's book and the Dobson-Lemon tables support this rule, which I still claim as a discovery.

Even without considering the distinction between immediate and eventual variety, the tables yield the following. The 39 species are considered in order of increasing repertoire-sizes. Dividing them into 3 groups, #1-13, 14-26, 27-39, and considering the pause lengths in each group we have:

<table>
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<th>Group</th>
<th>Group I</th>
<th>Group II</th>
<th>Group III</th>
</tr>
</thead>
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<tr>
<td>Spp. with very short pauses (less than 1.5 secs.)</td>
<td>0</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Spp. with short pauses (less than 3 secs.)</td>
<td>2</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>Spp. with long pauses (more than 6 secs.)</td>
<td>8</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Average pause length</td>
<td>6.39</td>
<td>4.58</td>
<td>3.70</td>
</tr>
<tr>
<td>Average repertoire size</td>
<td>2</td>
<td>8+</td>
<td>26+</td>
</tr>
</tbody>
</table>

This exhibits the "negative correlation between interval length and repertoire size" that Dobson and Lemon concede. It supports my view that songbirds tend to escape monotony either by musical variety or by substantial (for a bird's brain) lapses from singing. Taking the question of immediate versus eventual variety into account would, I predict, further support this conclusion, though adequate data are lacking. Thus the Song Sparrow and Cardinal, with long pauses, could be put into Group I as, for the monotony question, limited in variety. The Song Sparrow, though with many songs, sings quite repetitively in the short run. Another qualification: counting distinguishable patterns on a spectrogram is not an accurate measure of variety. There is also the depth of the contrasts. The Rose-breasted Grosbeak is listed as pausing for 10 seconds and yet highly versatile, but to me the contrasts seem slight.
Dohson and Lemon take to lightly the crucial evidence that individuals of some species (e.g., the Eastern Pecue) sing at times with immediate variety and short pauses; at other times without immediate variety but with long pauses; and in no third way. Three groups of Nightingale Wrens (Microcerculus marginatus) of tropical America occur: in one every successive sound is on almost the same pitch and pauses are several seconds; in another every sound is on a different pitch, with very short pauses; and in a third the pitch changes about every other sound, with pauses of intermediate length. The monotony threshold has not been disproved, whatever qualifications may be needed. All three authors have done me a good turn by applying such careful consideration to the topic.

To write in detail about hundreds of birds without mistakes is scarcely possible. Lark Sparrows do not "always," perhaps not even usually, sing in flight, and even the Skylark may sing from a perch. Borror is miscited (p. 70) as writing that a Carolina Wren has a singing-rate of 4-24 motifs per minute. What he correctly wrote was not motifs but songs. Bondesen's alteration underestimates by 3 times the amount of singing per minute. However, such mistakes seem relatively few.

My conclusion is that students of bird song need this book. We can be grateful that the author dared to undertake such a difficult task. It is the outstanding, up to date regional study of bird song. Although slightly too big for some jacket pockets, it is reasonably convenient to carry in the field as an aid to identification.—CHARLES HARTSHORNE.

JOHN GOULD BIRD PRINT REPRODUCTIONS. By Gordon C. Sauer. Privately printed; order from Richland Enterprises, P.O. Box 7062, Kansas City, MO., 64113; 76 pp., paper cover. $4.50.—This is not a collection of Gould's prints. Instead, its purpose "is to assist others in correctly identifying the origin of a particular Gould bird print. This information should be especially valuable for interior decorators, print dealers, and the many others who appreciate the beautiful colored prints of Gould's birds."—R.J.R.


THE BIOLOGICAL AND TAXONOMIC STATUS OF THE MEXICAN DUCK. By John P. Hubbard. Bulletin no. 16, New Mexico Dept. of Game and Fish, 1977:56 pp. No price given.—Based on an analysis of plumage and other characteristics, Hubbard concludes that the Mexican Duck is a subspecies (diazi) of the Mallard (Anas platyrhynchos) and not a separate species. The distribution and biological characteristics of the Mexican Duck are discussed, and recommendations are made concerning future management policies.—R.J.R.
A Classification of the Tyrant Flycatchers (Tyrannidae). By Melvin A. Traylor, Jr., Bull. Mus. Comp. Zool., Harvard Univ., Vol. 148, No. 4: 129–184, 1977. No price given.—This paper is an explanation of the new classification of the Tyrannidae that Traylor has prepared for volume 8 of Peters’ Check-list of Birds of the World. It is based on examination and measurements of study skins, as well as on distribution, behavior, and other information from the literature. The most important references used are Peter Ames’ study of the syrinx (Peabody Mus. Nat. Hist. Bull. 37, 1971) and Stuart Warters’ unpublished thesis on the cranial osteology of the Tyrannoidea (Louisiana State University, 1965). The last classification of the whole family was published by Hellmayr in 1927. The family includes all of Hellmayr’s genera plus 5 genera formerly classified in the Cotingidae, and Corythopis from the former family Conopophagidae. The 7 subfamilies of Hellmayr have been reduced to 3, the Elaeniinae, Fluvicolinae, and Tyranninae. The genera in each subfamily are listed in order from generalized to specialized types. Since this is often vague and arbitrary Traylor has simply retained Hellmayr’s sequence (in reverse) unless there are compelling reasons for change. Thirty-six of Hellmayr’s genera are synonymized, one is resurrected, and a new genus Zimmerius is described for 5 species formerly in Tyranniscus. The classifications of previous authors are contrasted, and the reasoning behind the new classification is given in lengthy detail.

An attempt is made to analyze the phylogeny of the Tyrannidae by cladistic analysis but is only marginally successful. Most characters are so variable and subject to such frequent convergence that their primitive and derived states could not be established. Only Warter’s data on the skull are so analyzed. The methods used to determine morphocline polarities are described only vaguely. They appear to be based on the idea that character states widely distributed among more than one subfamily are primitive, and on an intuitive assumption that primitive flycatchers were small arboreal forms, nearest the present Elaeniinae. The phylogenetic diagram (Fig. 7, p. 173) has a low degree of resolution. Four separate lineages arise from a hypothetical common ancestor, one to the Becards and Tityras, and the others to the 3 subfamilies. The lineages to the Tyrannidae and Fluvicolinae each branch into two groupings. This low resolution clearly demonstrates the need for additional studies with other kinds of data, a point that Traylor emphasizes several times. Nevertheless, there is an encouraging degree of correspondence between Ames’, Warter’s, and Traylor’s groupings. This indicates that the arrangements, as far as they go, are soundly based.

A new classification of the Tyrannidae has been sorely needed because of the abundance of new information that has accumulated in the half century following Hellmayr’s work. Traylor’s thorough study fills this need admirably to the degree that present knowledge permits, and will serve as a solid basis for the new studies that we may hope it will stimulate.—Robert J. Raikow.
ORNITHOLOGICAL NEWS

AARON M. BAGG STUDENT MEMBERSHIP AWARDS

Student Membership Awards in the Wilson Ornithological Society have been made available through funds generously donated in memory of the late Aaron M. Bagg, former president of the Society. The Student Membership Committee has designated the award recipients for 1978 as follows: Gary R. Alten, California State Polytechnic University; Darrel C. Boone, University of Maryland; Michael C. Delesantro, New Mexico State University; Claire L. Filemyr, Virginia Commonwealth University; Wayne Hoffman, University of South Florida; Anthony H. James, San Francisco State College; Samuel F. Jojola, New Mexico State University; Thomas R. Kemp, University of Toledo; Sandra J. Korowotny, Texas A&M University; Marc D. Longwood, California State University, Sacramento; Selby R. Mohr, California State University; Erica Nol, University of Guelph; Christopher M. Rogers, University of Wisconsin, Milwaukee; Kathryn J. Schneider, Princeton University; Theodore R. Simons, University of Washington; Thomas W. Smith, Jackson, Kentucky; Shirley J. Thompson, University of Toronto; Melinda J. Welton, University of Connecticut.—James R. Karr, Chairman, Student Membership Committee.

1978 ANNUAL MEETING

The 59th annual meeting of The Wilson Ornithological Society will be held at Jackson’s Mill, West Virginia, on 4–7 May 1978. The meeting will be hosted by the Brooks Bird Club, the Department of Wildlife Biology of West Virginia University, and West Virginia University.

A special feature of the meeting will be a symposium titled, “Resource Use Strategies in Birds,” to be held on the afternoon of Friday, May 5th. The symposium is organized by Dr. Elliot J. Tramer. The chairman of the Local Committee is Dr. Robert Whitmore, Division of Forestry, West Virginia University, Morgantown, WV 26506.

NOTICE OF A POSSIBLE NUMERICAL CODING SYSTEM FOR ALL BIRD SPECIES

Increased use of computers to store and process data about birds has precipitated a number of problems. One such problem is that of identifying the species (or higher taxonomic unit) under consideration. Many local ornithological organizations have solved this problem by identifying each species in their area with a unique code number (AOU number, for example). The proliferation of local systems could be avoided by development of an internationally recognized coding system for all bird species. The advantages of a standard system include international compatibility of records and facilitation of exchange of data and literature among countries.

Any new system must be taxonomically based, flexible enough to accommodate new species and taxonomic revisions, and be expandable for those interested in subspecific classification. For purposes of discussion, the following system is proposed. A worldwide numerical system will be based on Morony, Bock, and Farrand (Reference List of the Birds of the World, 1975, AMNH) with six digit numbers identifying each species. Thus, each genus has numbers reserved in advance for up to 99 species and searches of data can be made rapidly and efficiently by computer for any taxonomic level. Individuals wanting subspecific identifications can simply add one or two digits to the 6-digit base.

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THE WILSON BULLETIN

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SUGGESTIONS TO AUTHORS

See Wilson Bulletin, 87:144, 1975 for more detailed "Suggestions to Authors." Manuscripts intended for publication in The Wilson Bulletin should be submitted in duplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411-419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the back of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

NOTICE OF CHANGE OF ADDRESS

If your address changes, notify the Society immediately. Send your complete new address to the Treasurer, Ernest E. Hoover, 1044 Webster St., N.W., Grand Rapids, Michigan 49504. He will notify the printer.

The permanent mailing address of the Wilson Ornithological Society is: c/o The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

* See Ornithological News, p. 158, for address for ms submission.
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Head patterns of Mexican Piculus. From top to bottom: 1. "Typical" auricularis. 2. Variant auricularis with red flecks surrounding pileum. 3. Rubiginosus (either yucatanensis or maximus), with conspicuous red band surrounding pileum. 4. Variant aeruginosus with thin red line from lore to above the eye. 5. "Typical" aeruginosus with red restricted to the nape. Watercolor by George M. Sutton.
A REVISION OF THE MEXICAN PICULUS (PICIDAE) COMPLEX

Luis F. Baptista

The neotropical woodpeckers of the genus Piculus are closely related to the flickers (Colaptes) (Short 1972). Piculus species range from Mexico to southern Brazil, Paraguay, Peru (Ridgway 1914) and Argentina (Salvin and Godman 1892). Peters (1948) lists 46 taxa (9 species and their subspecies) of which 20 are subspecies of Piculus rubiginosus, the most widely distributed species. The latter ranges from southern Veracruz to the northwestern provinces of Jujuy, Salta, and Tucuman in Argentina (Peters 1948).

Compared with other picids, this genus is generally poorly represented in museum collections. It is possible that they are not as rare as they seem, but being rather silent and secretive birds and difficult to distinguish from the associated vegetation due to their cryptic green coloration, are easily passed unnoticed by collectors in the field.

A difference of opinion exists among taxonomists regarding the status of several of the Mexican forms. Two species complexes are recognized in the Mexican check-list (Miller et al. 1957). The Piculus auricularis complex is reported by these authors as consisting of 2 subspecies: sonoriensis known only from the type series of 3 birds taken at Rancho Santa Barbara, Sonora, and the nominate race auricularis recorded as ranging from Sinaloa south to Guerrero. They point out the uncertain status of the form sonoriensis, stating that additional material is needed to substantiate it. In their treatment, the Piculus rubiginosus complex in Mexico is subdivided into 3 subspecies: aeruginosus, maximus, and yucatanensis. Other authors have treated aeruginosus as a full species (Ridgway 1914, Peters 1948, Sutton 1951, Blake 1953, Peterson and Chalif 1973, Gehlbach et al. 1976). Wetmore (1941) questioned the status of maximus stating that “the systematic understanding of the species rubiginosus is at present unsatisfactory. In Mexico and Central America these birds seem subject to much individual variation, and I am inclined to believe that too many races have been proposed.” In discussing the status of yucatanensis, Miller et al. (1957) point out that “all
specimens from high altitudes in the interior of south central Mexico require critical re-examination."

This study treats morphological variation in the Mexican *Piculus* complex and evaluates the status of the described forms. *Piculus auricularis* so far has proved to be allopatric in its geographical distribution with the *rubiginosus* complex. Several authors (Van Rossem and Hachisuka 1937, Sutton 1951, 1953) have pointed out the similarities existing between these species suggesting that they might actually be conspecific. Is the genus *Piculus*, therefore, represented by 1, 2, or 3 species in Mexico?

**MATERIALS AND METHODS**

Museum samples of *Piculus (rubiginosus) aeruginosus* and *Piculus rubiginosus yucatanensis* allopatric throughout most of their ranges were examined critically. Specimen material from central Veracruz was scrutinized for evidence of free inter-breeding and intergradation which if present would justify the treatment of *aeruginosus* as a race of the *rubiginosus* complex, and if absent would warrant recognizing them as 2 distinct species. Material representing populations of *Piculus rubiginosus* in southern Mexico, namely in Oaxaca, Chiapas, and southern Veracruz, was analyzed, and the validity of the races *yucatanensis* and *maximus* evaluated.

For simplicity's sake the races of *Piculus rubiginosus* are referred to throughout this paper by their subspecific names *aeruginosus*, *yucatanensis*, and *maximus*. Similarly the races of *Piculus auricularis* are referred to as *auricularis* and *sonoriensis*. Some 238 skins from Mexico were considered in this study: 68 of *Piculus auricularis*, 81 of *aeruginosus*, 33 of *yucatanensis*, and 56 of *maximus*. In addition, 13 skins of *yucatanensis* from Honduras were examined. Localities from which samples were examined are illustrated in Fig. 1.

Measurements were taken of bill length (from nostril), tarsus, and chord of wing as described by Baldwin et al. (1931). Except when otherwise mentioned, one-tailed t-tests were conducted to test for differences between adjacent samples.

**ECOLOGY AND LIFE HISTORY NOTES**

Short (1973) has called attention to the paucity of information regarding the biology of *Piculus* species. I have, therefore, brought together the scanty literature on the natural history of the Mexican forms, which, hopefully, may prove useful to investigators intending to carry on field work on this group.

In the northernmost part of its range in Sonora, *Piculus auricularis sonoriensis* is known only from its type locality in the Upper Sonoran Zone at 1500 m elevation (Van Rossem 1945). Vegetation found in this life zone is discussed in Orr (1966:274). Elsewhere in its range it is a bird of pine-oak, pure oak, or oak-tropical deciduous forest. Specimens I examined were taken in pine-oak as high as 1970 m in Babizos, Sinaloa, to as low as 900 m in oak woodland near Tepic, Nayarit. To my knowledge it has never
been taken in the thorn scrub of coastal western Mexico. Much forest land has been cleared for cultivation; if abandoned, fallow land is invariably invaded by thorn scrub so that Piculus habitat is fast decreasing. In the southernmost part of its range in the Sierra de Miahuatlán, Oaxaca, the nominate auricularis has been taken in a greater variety of habitats such as boreal forest at 2650 m, cloud forest at 1500–2100 m, oak-tropical deciduous forest at 770 m, and humid tropical evergreen forest at 740 m. Habitats in these collecting localities are described in detail by Rowley (1966). The species probably occupies similar habitat in Guerrero (see vegetation map in Leopold 1959).

The Mexican Piculus, like others of this genus, in general are rather silent and secretive birds. The chief distinguishing feature between Colaptes and Piculus is the latter's silent nature (Short pers. comm.). There seems to be nothing in the literature concerning the vocalizations of Piculus auricularis or its nesting habits. Schaldach (1963) comments on the “apparent rarity”
of this species, suggesting that this may be due to its being very widely distributed, each individual covering a larger territory than those held by other woodpecker species.

**Piculus rubiginosus aeruginosus** has been taken in pine-oak 1500–2100 m in Nuevo Leon and in tropical forest in Gomes Farias, Tamaulipas (Sutton and Pettingill 1942). C. C. Lamb (unpubl. field notes, Moore Laboratory of Zoology) took a series of this form 24 km southwest of Linares, Nuevo Leon, where the habitat consisted of white and live oaks with mesquite trees forming an understory. This bird was also found to be fairly common in the canyon bottoms of the Sierra de Tamaulipas below 600 m and occasionally in pine-oak woods at 900 m (Martin et al. 1954). At La Joya de Salas, Tamaulipas, it was mainly a bird of deciduous woodland (Robins and Heed 1946). C. C. Lamb (unpubl. field notes) took this form on cottonwoods at the Rio Corona, 25 km north of Ciudad Victoria, Tamaulipas. There the vegetation consisted of sizeable trees intermixed with various cacti and mesquite trees. In the southern part of its range at Huachinango, 360 m, near the Puebla-Veracruz line, Lamb (field notes) collected this subspecies in “dense jungle.”

The subspecies **P. r. yucatanensis** is a bird of mesic conditions (Wetmore 1943:222), similar to *aeruginosus* in Puebla and Veracruz. In the rainforests of the Catemaco Basin of Veracruz, it was found to be mostly a forest edge species (Edwards and Tashian 1959). At Cordoba, Veracruz, 270 m, Lamb (field notes) took this subspecies in heavily wooded mountains, described as a tangle of vines and bushes.

The subspecies **P. r. maximus** inhabits more open forest, such as the pine-oak and riparian tropical hardwood of the Monseratte Plateau (Edwards and Lea 1955). At Finca Cacahuatl, Chiapas, 19 km east of Tapanatepec, Oaxaca, Lamb (field notes) found this species in pine and oak forests at 808 m.

Dickey and Van Rossem (1938) found that **P. r. yucatanensis** fed exclusively on insects. They described its foraging behavior as working slowly up a tree and gently prying into crevices. Wetmore (1968) studied the species in Panama where he found that the diet included fruit. He observed a male eating a large blackberry. C. C. Lamb (field notes) observed a female **P. auricularis** eating berries off a madrone tree at Babizos, Sinaloa.

**Piculus rubiginosus** is very flicker-like in many of its habits such as in vocalizations (Dickey and Van Rossem 1938, Sutton 1951, 1953, Blake 1953, J. S. Rowley pers. comm.), its manner of perching (Sutton 1951), and its courtship behavior as observed by Sutton (1942, 1953). The last author reported seeing 3 or 4 birds together with spread wings and tail, bobbing and bowing to each other while calling excitedly. This activity was interrupted with brief periods of statuesque motionlessness. Group displaying is also
known in at least 2 species of flickers, the Andean Flicker (Colaptes rupicola) and the Campo Flicker (C. campestris) (Short 1972).

Nest holes have been found from 3.6–9 m off the ground in dead and live trees (Sutton 1953, Skutch 1969, Rowley pers. comm.). Clutch size appears to be 4 in aeruginosus (Robins and Heed 1951), maximus (Rowley pers. comm.), uropygialis (Skutch 1956), and trinitatis (Belcher and Smooker 1936). Rowley took a set of 4 eggs of maximus at Cerro Baul, Oaxaca, 1300 m, in a nest in the cavity of a dead tree, 15 m above the ground by a creek (HC 21387). Lloyd Kiff kindly provided egg measurements (mm) which are as follows: 23.91 × 19.10, 24.39 × 19.20, 24.60 × 18.92, 23.43 × 18.29.

The only detailed observations on nesting behavior of P. rubiginosus are those of Skutch (1943, 1948, 1956, 1969) which are here summarized. Non-nesting individuals roosted solitarily in holes. A male was observed joining a female in her roosting hole which was converted to a nest. Four eggs were observed resting on clean chips. Both sexes alternated on the eggs during the day, and the male incubated by night. Three hatched together, and 1 the next day. The young were pink-skinned and naked on hatching. Pinfeathers were first observed at 8 days. The parents removed waste matter from the nest only until the young were old enough to take food from the nest entrance at approximately day 21. Both parents fed the young. Only one of a brood of 4 observed survived. This was a female nestling which was flushed from the nest at day 24 and flew off. An adult male used the nest hole for roosting after the young had fledged. Young in their first plumage already had markings of adults of their own sex.

**THE STATUS OF Piculus auricularis sonoriensis**

The subspecies sonoriensis was described by Van Rossem and Hachisuka (1937) as grayer on pileum and back than the nominate, with "the upper back between the nape and dorsum prominently barred with grayish white." The type locality given was Rancho Santa Barbara, 1500 m, 31.7 km north-east of Guirrocoba, situated at latitude 27° 16' and longitude 108° 35' (Van Rossem 1945).

The type and a topotype examined and compared with material from other parts of Mexico has led me to conclude that the gray coloration in the type description is of an adventitious nature rather than of genetic origin. The olive-green on the backs of Piculus is the result of the combined effect of 2 pigments distributed through 2 different components of the feathers. Beneath a dissecting microscope (10×) black pigment may be seen in the barbules, and yellow pigment in the rachis and barbs. Graying may be the result of any of a variety of causes such as feather wear, fading of yellow pigment due to exposure to light, to diet as suggested for Colaptes by Short (1965),
or the leaching effect of tannin from the barks of trees on which they forage as suggested for *Picoides stricklandi* by Davis (1965:573). Whatever the cause, graying as described for *sonoriensis* was also found in samples of *auricularis* from Nayarit and Oaxaca, as well as in several *rubiginosus*. The latter appeared darker due to heavier deposition of melanin pigment.

The second character mentioned by Van Rossem and Hachisuka, the barred upper back, was also found in series taken throughout the rest of the species' range. Moreover, a specimen taken in nearby Mount Mohinora in Chihuahua in October, in fresh fall plumage, was olive-green on the back as in *auricularis* from Sinaloa and Nayarit. The specimens from Sonora are, therefore, not subspecifically distinct at least from specimens taken in neighboring states such as Chihuahua, Sinaloa, and Nayarit as stated by these authors.

Birds from the northern states (Sonora to Colima) are larger than those from southern states (Guerrero and Oaxaca) (Figs. 2–4). Northern males have longer wings and bills and northern females have longer wings than do southern birds. Males of *sonoriensis* average 125 mm in wing length, and males of *auricularis* average 119.5 mm (one-sided \( p < 0.00005 \)). Mean wing length of female *sonoriensis* was 122.2 mm and that for female *auricularis* was 119.2 mm (one-sided \( p < 0.002 \)). Bills in male *sonoriensis* averaged 20.3 mm and those in male *auricularis* averaged 18.6 mm (one-sided \( p < 0.0005 \)).

The southern samples were also darker than the northern. This darkening was not dramatic and taken alone does not constitute a good distinguishing character. Hargitt (1890:183) gives measurements of the type specimen of the nominate *auricularis* taken in Xautipa, Guerrero, as follows: culmen 23.5 mm, wing 117 mm, tail 72 mm, and tarsus 20.8 mm. These figures suggest that Hargitt's type may be placed with the southern samples. The northern samples representing material from Sonora to Colima may be recognized as a race distinct from the nominate being slightly lighter in coloration, and larger in some morphometric characters discussed earlier. These must be known as *Piculus auricularis sonoriensis* Van Rossem and Hachisuka. The nominate race is, therefore, restricted to Guerrero and Oaxaca as far south as Pochutla on the road to Puerto Angel from Oaxaca City.

Schaldach (1963) recorded the first specimens of this species for the state of Colima. The bird from Chihuahua reported herein (H.C. \( \delta \) 4728) is believed to be the first record for that state. The material from Pochutla, Oaxaca (DM \( \delta \) 25046, DM \( \varphi \) 25045, DM \( \varphi \) 38824) extends the range of the species from its former southern range in Guerrero (Miller et al. 1957). To date no specimens have been reported for the state of Michoacan.

The pine-oak forests of Jalisco continue on into Michoacan. However, a
belt of arid tropical scrub separates the Michoacan pine-oak forests from those in Guerrero (see map in Leopold 1959:16). *Piculus a. sonoriensis* is to be expected in Michoacan, but these populations are probably separated from those in the Sierra Madre del Sur (*auricularis*) by the xeric belt. It is conceivable, however, that if specimens from Michoacan are obtained, these may prove to be intermediate in size between the forms, in which case *sonoriensis* should be merged in *auricularis*.

**Piculus auricularis as a subspecies of *P. rubiginosus***?

I found no evidence of interbreeding between *P. auricularis* and *P. r. yucatanensis* from which it seems to be separated by the Isthmus of Tehuantepec. Although previous authors have described *auricularis* as being entirely devoid of red on the crown, there were vestiges of red pigment on the tips of the crown feathers bordering the pileum in varying amounts on some specimens that I examined from throughout the species’ range. Red spotting on the crown was described in a juvenile by Ridgway (1914) but is not necessarily limited to that age class. I interpret this as a recapitulation of an ancestral character indicating that *auricularis* is a derivative of the *rubiginosus* group to which it is similar in many other respects. An analogous situation may be found in the conure *Aratinga astec* which shows a tuft of orange feathering above the cere (Hardy 1966:66) suggesting a common ancestor with the orange-fronted *Aratinga canicularis*. I have never found a female of *Piculus auricularis*, however, showing any trace of red on the crown in contrast to females of the *rubiginosus* group which always have conspicuously red napes. The *rubiginosus* forms also have notably darker crowns than do *auricularis*. The pileum is slate-gray in the former and light-gray in the latter, although as a result of the color cline *auricularis* from the Sierra de Miahuatlán, Oaxaca, approach *yucatanensis* with regard to this character.

In some groups of birds, notably the parrots (Psittaciformes), small differences in color or color patterns are important in social recognition and may serve as effective isolating mechanisms between species (Hardy 1966, 1967). Experiments by Noble (1936) have demonstrated the importance of the malar stripe in sexual recognition of the common flicker. Jerome Jackson (pers. comm.) blackened the red nape patch on a male Downy Woodpecker (*Picoides pubescens*). Its mate treated the disguised male as another female and attacked it. Thus the presence (as in *Piculus rubiginosus*) or absence (*P. auricularis*) of a red nape patch may be an effective ethological isolating mechanism between the two forms should they ever prove to breed sympatrically.

Figs. 2–4 reveal a decreasing size cline from *sonoriensis* to *auricularis*;
Fig. 2. Variation in bill length in Mexican Piculus. Horizontal lines denote ranges, vertical lines means, with rectangles as 95% confidence intervals on each side of the mean. Black rectangles denote males, clear rectangles signify females. Numbers indicate sample sizes. Aeruginosus-n = northern aeruginosus from Nuevo Leon, San Luis Potosi, and Tamaulipas, and aeruginosus-s = birds from Puebla and Veracruz.

however, with regard to measurements of bill and tarsus, this does not continue into yucatanensis which shifts to the right, i.e. toward larger values. The 2 complexes probably formed a continuous population down the west coast of Mexico at one time and are now separated by a belt of tropical deciduous forest (see map in Leopold 1959:16). Isolated from populations south of the Isthmus, and thus without the genetic load of eastern Mexican and Central American moister habitat populations, the accumulation of micromutations has resulted in the evolution of the northern population into its present form with overall lighter coloration (probably an adaptation to more xeric conditions) and in which selection against red on the crowns of females has been complete and is almost so in males. The available, indirect evidence, therefore, indicates that Piculus auricularis should be treated as a full species distinct from rubiginosus. This is in agreement with the Mexican check-list (Miller et al. 1957).

THE TAXONOMIC STATUS OF Piculus aeruginosus

Authors who have treated the form aeruginosus as a distinct species distinguished it from the rubiginosus complex, and in particular from the subspecies yucatanensis which replaces it geographically in central Veracruz, on the basis of the following characters:
Fig. 3. Variation in wing length in Mexican Piculus. See Fig. 2 for explanation of figure.

(1) Whereas in rubiginosus red forms a complete border around the pileum (see frontispiece), it is "evanescent over the eye" in aeruginosus (Salvin and Godman 1892).
(2) The form aeruginosus is clear olive green on back, breast, and underparts, whereas rubiginosus is usually orange-olive in these areas.
(3) The form rubiginosus is banded below with narrow horizontal bands, whereas the transverse bands on the breast and belly of aeruginosus are wider and hastate or "V" shaped in pattern.
(4) The form aeruginosus is a larger bird than is rubiginosus (Blake 1953:290).

Similarities in aeruginosus and rubiginosus are (i) in color of pileum, the latter being slate-gray in both (Ridgway 1914, Blake 1953), and (ii) females of both forms are identical in head coloration, i.e. both have slate-gray pileums with red restricted to the nape region.

MENSURAL CHARACTERS

Males of aeruginosus average longer in bill length than rubiginosus (= P. r. yucatanensis) (Fig. 2), however, the difference is not statistically sig-
significant. Females of both forms have very similar bill lengths. Both sexes of *aeruginosus* are significantly larger in wing and tarsal length than *rubiginosus* (Figs. 3, 4). Although females of the 2 forms overlap in wing length, males do not. Although males of the 2 forms overlap in tarsus length, females do not. Males of northern *aeruginosus* (from Nuevo Leon, Tamaulipas, and San Luis Potosi) average longer in wing length than southern *aeruginosus* (from Puebla and Veracruz), but this difference is not statistically significant.

**HEAD COLORATION**

Hargitt (1890:32) described a male *aeruginosus* from "Atoyac, Mexico" with its crown color intermediate to the former and typical *rubiginosus* in having "red over the eye carried forward in a very narrow line to the base of the bill." Miller et al. (1957) refer to this specimen as having been taken in Atoyac, Guerrero. Although a locality by that name does exist in Guerrero, this would place it right in the middle of the range of *P. auricularis*. I think this is highly unlikely since no field investigators subsequent to Hargitt have reported *aeruginosus* for that state, yet several *auricularis* have been taken there. It is my belief that the Atoyac referred to is in fact near Orizaba in Veracruz (see Gazetteer in Loetscher 1959:19).

Lawrence Binford (pers. comm.) independently came to the same con-
clusion with different evidence. Along with *P. aeruginosus*, Binford found that the collector (Mrs. Smith) also collected *Celeus castaneus*, *Momotus lessoni*, *Trogon puella*, *Rhamphastos carinatos*, and other Atlantic species at Atoyac, making it unlikely that the latter is in Guerrero. I have examined Hargitt's (loc. cit.) specimen in the British Museum of Natural History (BM 98-3-10-130) and have since found 13 other individuals possessing crowns with various amounts of red intermediate to "typical" *aeruginosus* and *rubiginosus*. The following scoring system has been devised to describe variation in crown color:

**Score**

1. Red nuchal patch continuing to just behind or immediately over the eye ("typical" *aeruginosus*).
2. Red nuchal patch as in #1 but some small flecks of red in front of eye or over lore.
3. Red nuchal patch as in #1 but thin red line from above eye to the base of the bill [as in Hargitt's (1890) specimen].
4. Red nuchal patch with pileum conspicuously surrounded by red ("typical" *rubiginosus*).

Data on crown color are summarized in Table 1. Two of 3 males taken 48 km east of Huachinango, Puebla (9.5 km west from the Veracruz line) had intermediate (class 3) crowns. One male taken 4.75 km east of the road to Villa Juarez, Puebla, had a class 2 crown. One male taken at Presidio, 35 km south of Cordoba, Veracruz had an intermediate (class 3) crown. In all other characters it was typical of *rubiginosus*. Two other males taken 15.8 km away had crowns conspicuously surrounded with red; however, comparison with material taken farther south indicated that these 2 Veracruz males had less red surrounding the pileum than "typical" *rubiginosus*. Three other males from Veracruz with class 3 crowns included single individuals from Huatusco, Atoyac, and Tampico. Two males from Jalapa, Veracruz had class 2 crowns.

In addition to the intermediates taken in central Veracruz or the near vicinity, 5 other intermediates were examined from the more northern states. These include a male from Linares, Nuevo Leon (ML 42758) (crown class 2), 2 males from Rio Corona (ML 40289) and Ciudad Victoria, Tamaulipas (BM 98-3-10-124) (crown class 2), a male from above Ciudad Victoria, Tamaulipas (crown class 3) (BM 9-8-3-10-123), and a male taken 47.5 km east of Ciudad Maiz, San Luis Potosi (ML 32469) (crown class 2). A male taken 5 km north of Gomez Farias, Tamaulipas (HC 4586) has a class 3 crown.
Table 1
Number of Specimens of *aeruginosus* and Variants Showing Different Crown Color States

<table>
<thead>
<tr>
<th>State</th>
<th>Score</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nuevo Leon</td>
<td></td>
<td>4</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tamaulipas</td>
<td></td>
<td>6</td>
<td>2</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>San Luis Potosi</td>
<td></td>
<td>4</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Puebla</td>
<td></td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Veracruz</td>
<td></td>
<td>7</td>
<td>3</td>
<td>4</td>
<td>3*</td>
</tr>
</tbody>
</table>

* Series taken near Presidio, Veracruz.

These data indicate that birds with crown classes intermediate to *aeruginosus* and *rubiginosus* may be found through the entire distributional range of *aeruginosus*.

**BODY COLOR**

I found the color of the back to be a good index of general body coloration. The following scoring system was devised to study variation in back color.

2. Green back with a slight flush of yellow (reference specimen ML ♀ 54405, 27 km east of Tapanatepec, Chiapas).
3. Green back with darker yellow flush than #2. Sometimes darker orange tips to feathers of back (reference specimen ML ♀ 45499, Finca Cacahuatl 24 km northeast of Tapanatepec, Chiapas).
4. Orange-green back, darker than #3 (reference specimen ML ♂ 35271, Socoltenango, Chiapas).

Back classes 1 and 2 represent “typical” *aeruginosus* and back class 4 “typical” *rubiginosus* (= *P. r. yucatanensis*). Data on back scores are summarized in Table 2. It may be seen that in the northern parts of its range, *aeruginosus* tends to be lighter, whereas in the south it is darker.

A female *aeruginosus* from Papantla, Veracruz, had a back score of 3. Another female from Poza Rica was given a back score of 3 but tended towards a 2. A male from Puebla and a male from Linares, Nuevo Leon also had back scores of 3. Three of a series of 6 *rubiginosus* taken at Presidio, Veracruz and 3 birds from Tenozapà, Veracruz had back scores of 3. Thus, in central Veracruz and nearby Puebla, individuals of the form *aeruginosus* may be similar in back color to some individuals of *rubiginosus*. Moreover,
Table 2
Back Color in *aeruginosus* and *yucatanensis*

<table>
<thead>
<tr>
<th>State</th>
<th>Score</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
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<tr>
<td>Nuevo Leon</td>
<td>5</td>
</tr>
<tr>
<td>Tamaulipas</td>
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<td>San Luis Potosi</td>
<td>10</td>
</tr>
<tr>
<td>Puebla</td>
<td>0</td>
</tr>
<tr>
<td>Veracruz-1</td>
<td>1</td>
</tr>
<tr>
<td>Veracruz-2*</td>
<td>0</td>
</tr>
</tbody>
</table>

* "Pure" *yucatanensis* from contact areas.

The darker *rubiginosus*-like back (class 3) appeared as far north as Nuevo Leon.

**Pattern of Barring on Breast and Belly**

The proportion of hastate spotting to barring and the width of the bars on breast, belly, and sides vary greatly in *aeruginosus*. The following 3 point scoring system was devised to study pattern of barring on the undersides of *aeruginosus*.

1. V or U shaped bands on entire breast, upper parts of belly, and sides (reference specimen ML ♀ 42961, Linares, Nuevo Leon, see Fig. 5).
2. V or U shaped bands restricted to upper breast. Lower breast and all or almost all of belly and sides with horizontal bands. Yellow bands often narrower than in #1 (reference specimen ML ♂ 32469, Ciudad Maiz, San Luis Potosi).
3. Horizontal bands on entire breast, belly, and sides. Yellow bands as narrow or narrower than in #2 (reference specimen ♂ 51606, Huatusco, Veracruz).

Barring class 3 represents the condition in "pure" *rubiginosus* (= *P. r. yucatanensis*). Barring class 2 represents the intermediate form, and class 1 the "pure" *aeruginosus*. In class 1 the pattern on the underside gives one the impression of yellow spots or scales. Sometimes the shapes of the bars in breast types 1 and 2 are similar to those in *Piculus auricularis*, a fact noted earlier by Salvin and Godman (1889). Bars in *auricularis* are horizontal, each band divided in the center by a very small V. Banding scores are summarized in Table 3.

A male taken at Huatusco, Veracruz (ML 51606) was light green on the back (back score 2) with red stopping behind the eye, characters of *aerugi-
Fig. 5. This is a negative print to emphasize barring patterns on skins of *yucatanensis*, *aeruginosus*, and variants. From left to right: 1. ML ♀ 34809, typical *aeruginosus*, taken 30 miles east of Huachinango, Puebla. 2. ML ♂ 40613, typical *aeruginosus*, taken at Rio Corona, 18 miles north of Ciudad Victoria, Tamaulipas. 3. ML ♂ 32469, variant *aeruginosus* with horizontal bars intermixed with hastate patterning, taken 30 miles east of Ciudad Maiz, San Luis Potosí. 4. ML ♂ 51606, variant *aeruginosus* completely barred below as in *yucatanensis*, taken 9 miles south of Huatusco, Veracruz, Mexico. 5. ML ♀ 45492, typical *maximus* for comparison, taken 15 miles northeast of Tapanatepec, Chiapas, Mexico.

*rubiginosus*. It was, however, indistinguishable in banding pattern from pure *rubiginosus*.

A female taken at Jalapa, Veracruz (AM44069) was almost entirely barred below with horizontal (*rubiginosus*) bands. Only a few very small U-shaped spots on its upper breast indicate some *aeruginosus* ancestry. It was, however, *aeruginosus* green (back score 2) on its back. A similar female taken at Cordoba, Veracruz, is in the collection of the British Museum of Natural History (BM 1857-7-30-1). It was taken with a male bearing the hastate markings of a "pure" *aeruginosus* (BM 1857-7-30-5) on the breast with the belly by degrees coming close to *rubiginosus*-type barring (Goodwin in litt.). A male taken at La Gloria, 15.8 km northwest of Presidio, Veracruz, (1 of a series of 3 males and 1 female) had a banding pattern reminiscent of *aeruginosus* in being almost scale-like. The other 3 birds had typical *rubiginosus* horizontal bands.
It is clear that individuals with banding patterns intermediate to *aeruginosus* and *rubiginosus* (Table 3) may be found in all but one state, Nuevo Leon. Moreover, 3 individuals had banding patterns indistinguishable from "pure" *rubiginosus*.

Ridgway (1914) records both *rubiginosus* and *aeruginosus* from Mount Orizaba. He also reports an *aeruginosus* from Cordoba, Veracruz; a variant described above was taken 55.4 km from this town. Additional variants taken at Cordoba in the collection of the British Museum have been described earlier. Lowery (1951) reports taking an *aeruginosus* at Portrero Viejo, 31.6 km from Presidio, Veracruz. I have described variant and "pure" *rubiginosus* taken 15.8 km from Presidio. Specimens showing characters typical or intermediate to both forms in various combinations have been found throughout the range of *aeruginosus* (Tables 1–3). This suggests that the latter has not differentiated completely from *rubiginosus* and must be regarded as a race of this species following Miller et al. (1957).

**VARIATION IN P. r. yucatanensis AND P. r. maximus**

Griscom (1929) described the race *maximus* from Guatemala as a larger bird than *yucatanensis* and greener throughout, lacking the "golden brown wash" of the latter race. Miller et al. (1957) included *maximus* in the Mexican check-list restricting its range in Mexico to the Pacific slope of extreme southeastern Oaxaca and adjacent Chiapas highlands at moderate altitudes.

*P. r. maximus* is separable from *yucatanensis* on the basis of wing length in both sexes (Fig. 3). Wing length in male *maximus* averaged 130.8 mm and that in *yucatanensis* averaged 119.2 mm (one-sided p < 0.00005). Mean wing length in female *maximus* was 128.1 mm and that in female *yucatanensis* was 117.0 mm (one-sided p < 0.00005).

*yucatanensis* are highly variable in coloration. The same 4-point scoring system used to study color variation in *aeruginosus* was used to study color variation in *yucatanensis* and *maximus* (Table 4). Back color was again
took as a rough index of general body color. A score of 4 indicated a typical *yucatanensis* and a score of 3 or less a typical *maximus*.

The difference in color scores (Table 4) between my large-winged samples and my small-winged samples is significant ($p < 0.0001$, Wilcoxon). However, since there is a great overlap in scores, color alone is not a good character to separate the races.

Presidio, Tenozapa, and La Gloria, Veracruz are in the vicinity of the zone of contact between *yucatanensis* and *aeruginosus*. Six lighter birds from these localities (scores 3 or tending towards 2, Table 4) may be indicative of introgression of *aeruginosus* genes. Similarly, a light bird from Comitan (1 of 4) may reflect some *maximus* genes. However, 5 lighter colored birds from Catemaco, Matias Romero, and Tumbala (scores 2 to 3) are probably illustrative of the erratic type of color variation in *yucatanensis* remarked on by Griscom (1929).

One *maximus* from near Tapanatepec, Chiapas (scores 3–4) and 2 dark birds from Socotenango (Table 4) may reflect some *yucatanensis* ancestry. However, 1 dark bird from Catemaco, Las Palmitas, Honduras. Red may also invade the top of the pileum in various degrees. These observations suggest that the *P. rubiginosus* complex shared a common ancestor with *Piculus rivoli*; the latter as a red-backed species variable in the amount of this pigment on the pileum and back and with patterns below suggesting *rubiginosus*.

### SIZE DIMORPHISM BETWEEN THE SEXES

Size dimorphism between the sexes was computed as percent difference in mensural characters between males and females and coefficient of difference (Mayr et al. 1953).
Table 5
SEXUAL DIMORPHISM IN PICULUS

<table>
<thead>
<tr>
<th></th>
<th>%</th>
<th>c.d.</th>
<th>% joint nonoverlap</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>BILL</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>sonoriensis</td>
<td>15.4</td>
<td>1.3</td>
<td>91</td>
</tr>
<tr>
<td>auricularis</td>
<td>8.5</td>
<td>0.65</td>
<td>&lt;75</td>
</tr>
<tr>
<td>aeruginosus-N</td>
<td>12.1</td>
<td>1.3</td>
<td>91</td>
</tr>
<tr>
<td>aeruginosus-S</td>
<td>13.2</td>
<td>1.5</td>
<td>94</td>
</tr>
<tr>
<td>yucatanensis</td>
<td>6.2</td>
<td>0.55</td>
<td>—</td>
</tr>
<tr>
<td>maximus</td>
<td>7.4</td>
<td>0.70</td>
<td>&lt;75</td>
</tr>
<tr>
<td><strong>WING</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>sonoriensis</td>
<td>2.3</td>
<td>0.67</td>
<td>75</td>
</tr>
<tr>
<td>auricularis</td>
<td>0.18</td>
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<tr>
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<td>5.6</td>
<td>1.5</td>
<td>94</td>
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<td>yucatanensis</td>
<td>1.8</td>
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<td>—</td>
</tr>
<tr>
<td>maximus</td>
<td>2.1</td>
<td>0.38</td>
<td>—</td>
</tr>
<tr>
<td><strong>TARSUS</strong></td>
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</tr>
<tr>
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<td>0.35</td>
<td>—</td>
</tr>
<tr>
<td>auricularis</td>
<td>5.5</td>
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<td>1.1</td>
<td>87</td>
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<tr>
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<tr>
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<td>—</td>
</tr>
<tr>
<td>maximus</td>
<td>0.6</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

All samples are most dimorphic in bill length, as evidenced by percent difference in measurements and percent of joint nonoverlap (Table 5). Only in *yucatanensis* is dimorphism in bill length not significant. There is also a reduction in dimorphism from north to south, i.e. from *sonoriensis* to *auricularis* and from *aeruginosus* to *yucatanensis*. The difference in dimorphism between northern and southern samples of *aeruginosus* is small and probably due to sample error.

There is also a north to south reduction of dimorphism in wing length, from *sonoriensis* to *auricularis* and from *aeruginosus* to *yucatanensis*. The slight north to south reduction in dimorphism between the samples of *aeruginosus* is due to the slight north to south decrease in wing length in male *aeruginosus*.

Only northern *aeruginosus* are dimorphic in tarsus length. This again may be due to sample error.

Davis (1965:566) has suggested that "the evolution of accentuated sexual
dimorphism in a given character is one means of increasing the variability of the character in the population. But another method would be the evolution of accentuated individual variability within each sex in the character concerned, with presumed increased variability in diet.” Selander (1966) interprets dimorphism, especially in bill length, as adaptive radiation at the intra-populational level so that individuals may “occupy different subniches or adaptive subzones, subdividing and, perhaps, expanding the total zone or niche” used by the population. Kilham (1965), Selander (1966), and others (review in Hogstad 1976) have studied a variety of woodpecker species and found that either each sex fed on different species of trees, employed different methods of foraging, or fed on different portions of the same tree. However, Ligon (1968) studied Red-cockaded Woodpeckers (*Picoides borealis*) which were only slightly sexually dimorphic for bill size and found differences in foraging sites between the sexes. Subsequently, Ligon (1973) studied White-headed Woodpeckers (*P. albolarvatus*) with greater dimorphism in bill length (10%) than any other measurement and found no differences in foraging sites between the sexes. He cautioned, therefore, (Ligon 1973:867) that one cannot always predict foraging patterns by degree of sexual dimorphism in bill size. The Mexican forms of *Piculus* differ greatly in degree of sexual dimorphism in bill size, from 15.4% in *sonoriensis* or 13.2% in *aeruginosus* to almost none in *yucatanensis*. It is hoped that these data will encourage others to conduct ecological studies on this little known group.

**DISCUSSION**

In this treatment, all taxa of *Piculus* proposed in the Mexican check-list (Miller et al. 1957) are recognized, with, however, differences in the ranges of the subspecies of *P. auricularis* (Fig. 1). The western *auricularis* complex has been described as paler than the *rubiginosus* forms of the east and southeast. Buchanan (1964) has observed a similar situation for Least Pygmy Owls (*Glaucidium minutissimum*). This trend could probably also be found in other Mexican birds with similar distribution ranges.

Size decreases clinally from north to south (Figs. 2–4), i.e. from *sonoriensis* to *auricularis* and from *rubiginosus* to *yucatanensis*, a manifestation of Bergmann’s rule (Mayr 1942, James 1970, Mengel and Jackson 1977). The clines are steeper for males than they are for females for wing and bill length.

The tendency towards darker individuals in the southern parts of the ranges of both the *auricularis* and *rubiginosus* complexes is a manifestation of Gloger’s rule (Mayr 1942). Gloger’s rule may also be interpreted as the result of selection for crypticity. Selander and Giller (1963) discuss the color patterns found in *Melanerpes aurifrons*, pointing out
that "Boldly patterned types (M. a. aurifrons and M. a. polygrammus), which are in gross aspect much lighter than the narrowly barred types (M. a. dubius and M. a. santacruzi), are found in arid regions where light penetrates deep into the middle and lower strata of relatively open woodland vegetation, and the background of trunks and branches to which the woodpeckers are exposed is relatively light in color. But in more humid regions where denser broad-leaved vegetation creates greater areas of shadow and where the color of the vegetation tends to be darker, the dark appearance of the narrowly barred form is probably at a selective advantage. In similar fashion we assume that the value and hue of the color of the breast and sides are adaptive, providing effective counter-shading by being darker in more humid areas and lighter in those of greater aridity." Concomitant with color changes in the Piculus forms mentioned are also changes in the vegetation types as shown in Leopold's (1959) vegetation map of Mexico. In Chiapas both Bergmann's and Gloger's rules operate locally to produce the larger, lighter race maximus of the montane districts of the Pacific Cordillera and the smaller darker race yucatanensis of the Atlantic lowlands.

I have discussed the results of selection against red pigment on the crowns of aeruginosus and auricularis. This perhaps may be interpreted as selection for increased crypticity in areas of more open vegetation where bright colors would render them more conspicuous. It is noteworthy that in none of the forms is the red of the male malar stripes in any way affected. Noble (1936) has shown the importance of such malar stripes in sexual recognition in the Common Flicker (Colaptes auratus). It is probably because of a similarly important role as a social releaser that these stripes are retained in auricularis and aeruginosus.

**SUMMARY**

Variation in the Mexican representatives of the genus Piculus was studied in order to determine the status of the described forms (species and subspecies). A qualitative analysis of museum specimens representing population samples was presented along with quantitative data including statistical treatments of bill, wing, and tarsus measurements.

The status of Piculus auricularis sonoriensis Van Rossem and Hachisuka was discussed: the type and a topotype examined did not differ from samples taken in neighboring states as indicated by the authors. However, northern samples of Piculus auricularis from Sonora to Colima were separable from material from Guerrero and Oaxaca on the basis of size and color. Two races are thus recognized.

Variation in Piculus aeruginosus Malherbe was studied and evidence was presented suggesting genetic continuity and introgression with P. r. yucatanensis so that it is here regarded as a race of rubiginosus. Two races of Piculus rubiginosus are recognized for Chiapas, maximus of the Pacific Cordillera and yucatanensis of the Atlantic lowlands, separable on the basis of coloration and wing length.

All the forms of Piculus in the Mexican check-list (Miller et al. 1957) are thus recog-
nized with some changes in geographic distribution; these were divided into 2 species complexes including the gray crowned *auricularis* forms occupying the more xeric west and the slate crowned *rubiginosus* races of the more mesic east and southeast. In *aeruginosus* and *auricularis* size decreased clinally from north to south and intensity of coloration was found to increase in a clinal fashion in the same direction in accordance with Gloger's rule. Manifestation of Gloger's rule was discussed as being possibly the result of selection for crypticity. Both laws seem to operate locally in Chiapas to produce the larger, lighter colored highland race *maximus*.

Size dimorphism between the sexes was found to decrease from north to south in both species complexes. Size dimorphism was most pronounced in bill length in all but one form (*yucatanensis*). The possible ecological significance of these findings was discussed.

ACKNOWLEDGMENTS

My thanks first of all to Robert T. Orr who called my attention to this problem, and for all his advice and assistance in the preparation of this paper; to Jacqueline Schone-wald and my wife, Joyce, for their help and advice in the statistical methods; to Jerome A. Jackson, Ned K. Johnson, Edward Kessel, Lloyd Kiff, David Mullen, Robert T. Orr, and Lester L. Short for reading various versions of this manuscript and for their valuable suggestions; to the late Elwood Molseed for providing transportation to Mexico City where I examined some critical material and for his delightful companionship in the field.

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A grant from the California Academy of Sciences enabled me to do some field work in the Sierra de Miahualtan in Oaxaca in the summer of 1965. In the summer of 1966 an additional grant from the California Academy of Sciences and the courtesy of Dr. Elwood Molseed permitted more field work in Mexico and the visit to Dr. Allan Phillips' collection. A grant from the American Association for the Advancement of Sciences enabled me to visit the institutions in Southern California listed above. For making these grants available to me, my sincerest thanks to Drs. Robert T. Orr and George E. Lindsay.

Last but not least, I thank Dr. George M. Sutton for the beautiful colored plate which adds much to this paper.

LITERATURE CITED


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Baptista • REVISION OF MEXICAN PICULUS


DISTRIBUTION, DENSITY, AND PRODUCTIVITY OF ACCIPITER HAWKS BREEDING IN OREGON

RICHARD T. REYNOLDS AND HOWARD M. WIGHT

Density of nests and productivity of Sharp-shinned Hawks (*Accipiter striatus*), Cooper’s Hawks (*A. cooperii*), and Goshawks (*A. gentilis*) within Oregon are of interest because of recent declines of accipiter hawks in the eastern United States (Schriver 1969, Hackman and Henny 1971, Henny and Wight 1972). One factor implicated in this decline was contamination with chlorinated hydrocarbons (Ratcliffe 1970, Cade et al. 1971, Anderson and Hickey 1972, Wiemeyer and Porter 1970). Snyder et al. (1973) presented data on levels of DDE in eggs of accipiter hawks from various regions in North America, including Oregon. Their data indicated that eggs of each species are contaminated, but they were unable to evaluate the effects of contamination on populations in Oregon as historical data on the abundance of breeding accipiters did not exist.

This paper presents information on the distribution of nests, nesting density, and nesting success of Sharp-shinned Hawks, Cooper’s Hawks, and Goshawks in Oregon. In an attempt to assess current production trends, nesting densities and productivities of Oregon accipiters are compared to densities and productivities of accipiters elsewhere in North America and, where appropriate, in Europe.

METHODS

This study included a survey for accipiter nests in all major forest types in Oregon except the western juniper (*Juniperus occidentalis*) forests in central Oregon and the Sitka spruce (*Picea sitchensis*) forests along the northwest coast. Forests included in this survey contain a wide variety of tree species, though with few exceptions, conifers are dominant. These forests are primarily restricted to montane areas and vary from the extensive and continuous forests of the Coast and Cascade ranges to the disjunct forests of smaller mountain ranges east of the Cascades.

We divided Oregon into 3 subregions: (1) the Coast Range and the west slope of the Cascade Range, a moist, densely forested region with a mild maritime climate, referred to as western Oregon; (2) southwestern Oregon, which includes the Siskiyou Mountains, characterized by relatively warm, wet winters and hot, dry summers; and (3) eastern Oregon (including the east slope of the Cascade Range), a high elevation and more dry region with affinities to the Rocky Mountain forests. Franklin and Dyrness (1973) presented a list of the vegetational zones and associated tree species plus the edaphic and climatic characteristics of these sub-regions. Nesting success and distribution of nesting pairs of accipiters were determined during the breeding seasons of 1969 through 1974. During 1969 and 1970, all forest stands were searched for nests. However, after

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1 Deceased.
learning to recognize the structural characteristics of forest stands selected by each species for nesting, the amount of forest intensively searched was reduced. Searching only stands considered potential nest sites proved suitable for surveying large areas, but undoubtedly caused us to overlook some nests. Searches conducted during the 6 breeding seasons disclosed 117 nest sites and 139 attempts at nesting.

Nest density for each species was determined by intensively searching the Corvallis and Bly study areas. The Corvallis study area, 9281 ha, was located on the east slope of the Coast Range approximately 8 km northwest of Corvallis, Benton Co. (T. 10S and 11S; R. 5W and 6W) (Fig. 1). Elevation of this area ranged from 80 to 500 m and was of moderate relief. Except for some narrow valley bottoms (fenced pastures) and one burn in various stages of regeneration, the forests of this study area were continuous. Douglas-fir (Pseudotsuga menziesii) was the dominant tree species and it existed in pure stands or mixed with western hemlock (Tsuga heterophylla), red alder (Alnus rubra), or bigleaf maple (Acer macrophyllum). On some dry, south-facing slopes, small stands of Oregon white oak (Quercus garryana) persisted. A major portion of the Corvallis study area was composed of young (<100 years) stands of Douglas-fir, though stands of all age classes were represented. This area was searched during the nesting seasons of 1970 and 1971.

The Bly study area, 11,741 ha, was in the Gearhart Mountains approximately 24 km northeast of Bly, Lake Co. (T. 15E and 16E; R. 36S) (Fig. 2). Elevation of this area ranged from 1430 m to 2130 m and was also of moderate relief. Except for 2 burns which were in young regenerative stages and small natural openings, forests of this area were continuous. Tree species composition varied from pure stands of ponderosa pine (Pinus ponderosa) at lower elevations (southwest portion), through mixed stands of ponderosa pine and white fir (Abies concolor) at mid-elevations, to mixed and pure stands of white fir and lodgepole pine (Pinus contorta) at high elevations (north and east portions). Stands of all age classes in each timber type were represented; however, the most common type was mature ponderosa pine overstory with mixed understory of ponderosa pine and white fir. The Bly area was searched during the nesting season of 1974.

Data from these 2 areas also provided mean distances between nests of conspecifics. Since several researchers (e.g., Hoglund 1964) reported only distances between nests, we include a mean distance to make the dispersion of nests in our study areas comparable. We determined this by locating nests on maps and measuring the distance between each active nest and its nearest neighbor, using the distance between any 2 nests only once. Since some pairs used different nest sites from year to year, distances between nests were calculated on a yearly basis, using each nest as a single observation. Nest sites were visited up to 2 months after fledging to determine the length of time young remained in the nest area under care of the adults.

RESULTS AND DISCUSSION

Distribution of nesting pairs.—Of the 139 nesting attempts, 16 were Sharp-shinned Hawk. 42 were Cooper’s Hawk, and 81 were Goshawk.

All 3 species were found nesting in eastern, western, and southwestern Oregon. Sharp-shinned Hawks nested in the Coast and Cascade ranges, the Siskiyou, Gearhart, and the Steens mountains at elevations ranging from 120 m in the Coast Range to 2010 m in the Gearhart Mountains. Cooper’s Hawks nested in the Coast and Cascade ranges, the Siskiyou, Wallowa, and Gear-
hart mountains. This species also nested in the floor of the Willamette Valley (western Oregon) in isolated, but extensive stands of Douglas-fir. Elevations of Cooper's Hawk nests ranged from 15 m in the Willamette Valley to 1760 m in the Gearhart Mountains. Goshawks nested on both east and west slopes of the Cascade Range, the Siskiyou Mountains, and in all mountain ranges in eastern Oregon. Elevation of Goshawk nests ranged from 580 m on the west slope of the Cascades to 1860 m in the Gearhart Mountains. Nests of Goshawks were not found in the Coast Range.

The relative abundances of nests of each accipiter species in our statewide sample possibly reflected the relative difficulty of locating nests rather than their actual abundances. Goshawks, because of their large size, are the
Fig. 2. Bly study area. Illustrating main drainages and accipiter nest locations in 1974.

easiest to locate; whereas Sharp-shinned Hawks, the smallest accipiter in Oregon, are the most difficult. This bias in our sample makes it appear that Sharp-shinned Hawks are the least abundant of the Oregon accipiters, while the opposite may be true (see below). We feel that, with the possible exception of Sharp-shinned Hawks in Western Oregon, the relative density of each species in the Corvallis and Bly areas approximates the actual densities of nesting accipiters in each region.

Nest densities and spacing.—Portions of the Corvallis study area received a cursory nest search in 1969; 2 Cooper's and 1 Sharp-shinned hawk nests were located. Four Cooper's Hawk nests were located in 1970 and 5 in 1971 (Fig. 1), resulting in 1 nest per 2321 ha in 1970 and 1 nest per 1857 ha in 1971. Mean distance between nests was 5.0 km in 1970 (range = 3.7–6.3 km, SD = 1.29 km) and 5.5 km in 1971 (range = 4.8–6.9 km, SD = .97 km). No nests of Sharp-shinned Hawks were located in this study area in 1970 or 1971.
Table 1
Nest Site Tenacity of Accipiter Hawks in Oregon, 1969–1974

<table>
<thead>
<tr>
<th></th>
<th>Number of Years of Occupancy</th>
<th>R/Rb</th>
<th>Reoccupancy Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td><strong>Sharp-shinned Hawk</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of nest sites revisited</td>
<td>5</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Number of nest sites reoccupied</td>
<td>3</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>% reoccupancy</td>
<td>40</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Cooper’s Hawk</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of nest sites revisited</td>
<td>22</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td>Number of nest sites reoccupied</td>
<td>16</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>% reoccupancy</td>
<td>27</td>
<td>11</td>
<td>0</td>
</tr>
<tr>
<td><strong>Goshawk</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of nest sites revisited</td>
<td>35</td>
<td>17</td>
<td>7</td>
</tr>
<tr>
<td>Number of nest sites reoccupied</td>
<td>20</td>
<td>15</td>
<td>7</td>
</tr>
<tr>
<td>% reoccupancy</td>
<td>43</td>
<td>41</td>
<td>29</td>
</tr>
</tbody>
</table>

a Number of sites occupied for 1 year only.
b Number of sites reoccupied/number of sites revisited.

In 1974, 4 Sharp-shinned Hawk nests, 5 Cooper’s Hawk nests, and 4 Goshawk nests were located in the Bly study area resulting in an overall density of 1 nest per 903 ha or 1 Sharp-shinned Hawk nest per 2750 ha, 1 Cooper’s Hawk nest per 2200 ha, and 1 Goshawk nest per 2750 ha (Fig. 2). Mean distances between nests of conspecifics were: Sharp-shinned Hawks, 4.1 km (range = 1.8–6.0 km, SD = 2.12 km); Cooper’s Hawks, 3.5 km (range = 2.6–4.4 km, SD = .79 km); and Goshawks 5.6 km (range = 2.4–8.4 km, SD = 3.00 km) (Table 1).

Two Sharp-shinned Hawk nests were approximately 300 m from active Cooper’s Hawk nests, and 1 Sharp-shinned Hawk nest was approximately 450 m from an active Goshawk nest. Five Cooper’s Hawk nests were between 300 to 450 m from active Goshawk nests. In 2 of the latter cases, both species used the same nest sites for 2 consecutive years. In all the above situations, only 1 nest, a Sharp-shinned Hawk adjacent to a Cooper’s Hawk, failed to fledge young.

Mean distance between nesting pairs of Cooper’s Hawks in the Bly and Corvallis areas was considerably greater than the approximate 1.6 km between nests found in Arizona (N. Snyder pers. comm.) and in California (Fitch et al. 1946). Meng (1951) did not determine a mean distance between
30 nests of Cooper’s Hawks in New York, but reported that the 2 closest nests, on opposite edges of 2 extensive woods separated by a large field, were 2.4 km apart.

Mean distance between adjacent pairs of Goshawks in the Bly area was essentially the same as reported for European Goshawks (A. g. gentilis) in Sweden (5.5 km, range = 3.9–8.0 km) (Hoglund 1964). While McGowan (1975) did not report a mean distance between any of 9 active nests in Alaska, he found a density of 1 pair per 4869 ha in 1971 and 4142 ha in 1972, only half the density of Goshawks in Oregon. In Finland, a density greater than that in Oregon has been reported—1629 ha per pair (9 pairs) (Hakila 1968).

Nest site tenacity.—Nest sites of accipiters were defined as the portion of a forest stand containing the nest and the requisite structural features of the vegetation (density, height, canopy closure) and physiographic conditions (slope, aspect, surface water) used by a nesting pair during the breeding season. In Oregon, the area within a nest site increased with increasing accipiter size, ranging from approximately 4 ha for Sharp-shinned Hawks, 6 ha for Cooper’s Hawks and 8–10 ha for Goshawks.

Many established nest sites of each accipiter contained more than 1 nest. We did not observe Sharp-shinned or Cooper’s hawks reoccupying an old nest. If a pair of either species returned to a previously used site, a new nest, usually within 100 m of the old, was constructed. In contrast, many pairs of Goshawks used the same nest for 2 or more years or alternated between 2 or more nests within an established site. Alternate nests within an established Goshawk site varied from 15 to 150 m apart, though most were 60–90 m apart. In addition, several pairs of Goshawks had alternate nest sites, usually within 0.4 km, between which they shifted on a 1–3 year basis. In general, nest site tenacity increased with increasing accipiter size. The maximum number of years a nest site was occupied was 2 years for Sharp-shinned Hawks, 3 years for Cooper’s Hawks, and 5 years for Goshawks (Table 1).

For one reason or another an established pair of Goshawks may desert one nest site for another up to 3.5 km away. For example, in 1974 one pair of Goshawks on the Bly study area, which used one site for several years, moved 3.2 km north to a site which was approximately 2.1 km south of another active Goshawk nest. Since these hawks were not marked, we were not certain that both nest sites had been occupied by the same pair. However, frequent sightings of the male foraging within areas used in previous years and carrying prey from these areas toward the new site suggested that the same pair was involved. Nest site shifts of this type occasionally placed conspecific pairs in close proximity (less than 3.5 km apart), though none of these situations was found to persist for more than one breeding season.
Three shifts of nest sites, averaging 3.1 km (range = 2.6–3.2 km) were also noted for Cooper's Hawks in the Corvallis study area. Although not certain the same pairs were involved, we observed both single and pairs of hawks flying between old and new nest sites on several occasions before egg laying.

In 2 instances, nest sites of 1 species were occupied during subsequent breeding seasons by other species. The first of these involved a site used for 2 seasons by Sharp-shinned Hawks prior to its being used in the third year by Cooper's Hawks. Another involved a site used by Goshawks for 2 years prior to its being occupied by Cooper's Hawks. No interactions between pairs involved were noted.

Initiation of breeding and egg laying.—One pair of Goshawks was first noted in its nest site on 23 March, and most pairs were found in their sites by early April. In Oregon, the date of clutch completion and initiation of incubation by Goshawks was highly variable. The earliest clutch was completed about 10 April, and the latest, 2 June (Fig. 3). However, most clutches were completed and incubation began within the last week of April and the first 2 weeks of May, approximately the same period reported by McGowan (1975) for Goshawks in interior Alaska.

Regression analysis suggested little association between the date of initiation of incubation and the elevation of 30 Goshawk nests in Oregon, for all years combined as well as in any single year.

One pair of Cooper's Hawks was first noted in its nest site on 28 March (western Oregon), while most pairs throughout Oregon were observed in or about the nest sites by mid-April. In western Oregon, clutches were completed and incubation began during the last week of April through the third week of May, while those in eastern Oregon were completed during the third through the last week of May (Fig. 3). The earliest completed clutch for Cooper's Hawks was 1 May (western Oregon), and the latest, 30 May (eastern Oregon).

One pair of Sharp-shinned Hawks was first noted in its nest site on 9 May, 6 days before the first egg was laid. On this date the nest was complete, indicating that the hawks had probably been at the site for at least a week prior to 9 May. Clutches of Sharp-shinned Hawks were completed and incubation began sometime in May, although some may not be completed until mid-June (Fig. 3). The earliest completed clutch was 14 May and the latest 19 June.

Due to the narrow range of elevation over which we found nests within each subregion and because our sample of Cooper's and Sharp-shinned hawk nests is not continuous over the entire range of elevation from western to eastern Oregon (highest in western Oregon, 600 m; lowest in eastern Oregon, 1400 m), it was difficult to determine whether or not there was an association between elevation and date of nesting for these species. However, initiation
Fig. 3. Number of nests and approximate date of initiation of incubation in Sharp-shinned Hawk, Cooper’s Hawk, and Goshawk in Oregon, 1969-1974. Southwestern Oregon not shown due to insufficient number of nests.

of incubation in both species in eastern Oregon was somewhat later than in western Oregon (Fig. 3). In general, clutch size decreased as the size of accipiter increased (Table 2).

Incubation and nestling period.—In Oregon, the incubation period lasted 30–32 days for each accipiter species. This was about the same period reported by McGowan (1975) for Goshawks in Alaska (29 days). Bent (1937) listed 28 days for Goshawks, 24 days for Cooper’s Hawks, and 21–24 days for Sharp-shinned Hawks. Brown and Amadon (1968), who summarized much of the literature concerning birds of prey, reported incubation periods of 36 days for Cooper’s Hawks and 34–35 days for Sharp-shinned Hawks.
<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>Mean number of eggs</th>
<th>Mean number of eggs hatched</th>
<th>Mean number of young fledged/nest attempt</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Sharp-shinned Hawk</strong></td>
<td>1969</td>
<td>5.0 (3)(^a)</td>
<td>3.7 (3)(^a)</td>
<td>2.3 (3)(^a)</td>
</tr>
<tr>
<td></td>
<td>1970</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>1971</td>
<td>3.0 (1)</td>
<td>1.0 (1)</td>
<td>.5 (2)</td>
</tr>
<tr>
<td></td>
<td>1972</td>
<td>5.0 (1)</td>
<td>4.0 (1)</td>
<td>4.5 (2)</td>
</tr>
<tr>
<td></td>
<td>1973</td>
<td>—</td>
<td>—</td>
<td>4.0 (1)</td>
</tr>
<tr>
<td></td>
<td>1974</td>
<td>—</td>
<td>—</td>
<td>3.0 (3)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td>4.6 (5) (0.89)(^b)</td>
<td>3.2 (5) (1.30)(^b)</td>
<td>2.7 (11) (1.74)(^b)</td>
</tr>
<tr>
<td><strong>Cooper’s Hawk</strong></td>
<td>1969</td>
<td>4.3 (4)</td>
<td>4.0 (4)</td>
<td>2.0 (3)</td>
</tr>
<tr>
<td></td>
<td>1970</td>
<td>4.0 (1)</td>
<td>4.0 (1)</td>
<td>3.3 (3)</td>
</tr>
<tr>
<td></td>
<td>1971</td>
<td>3.8 (4)</td>
<td>2.0 (4)</td>
<td>1.6 (7)</td>
</tr>
<tr>
<td></td>
<td>1972</td>
<td>3.5 (4)</td>
<td>2.3 (4)</td>
<td>2.0 (7)</td>
</tr>
<tr>
<td></td>
<td>1973</td>
<td>—</td>
<td>—</td>
<td>2.5 (2)</td>
</tr>
<tr>
<td></td>
<td>1974</td>
<td>—</td>
<td>—</td>
<td>2.0 (2)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td>3.8 (13) (1.14)</td>
<td>2.8 (13) (1.91)</td>
<td>2.1 (24) (1.56)</td>
</tr>
<tr>
<td><strong>Goshawk</strong></td>
<td>1969</td>
<td>—</td>
<td>—</td>
<td>1.5 (2)</td>
</tr>
<tr>
<td></td>
<td>1970</td>
<td>3.5 (2)</td>
<td>3.0 (2)</td>
<td>1.8 (4)</td>
</tr>
<tr>
<td></td>
<td>1971</td>
<td>3.0 (2)</td>
<td>2.0 (2)</td>
<td>1.6 (5)</td>
</tr>
<tr>
<td></td>
<td>1972</td>
<td>3.0 (1)</td>
<td>3.0 (1)</td>
<td>1.9 (22)</td>
</tr>
<tr>
<td></td>
<td>1973</td>
<td>—</td>
<td>—</td>
<td>1.5 (11)</td>
</tr>
<tr>
<td></td>
<td>1974</td>
<td>—</td>
<td>—</td>
<td>2.0 (4)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td>3.2 (5) (0.45)</td>
<td>2.6 (5) (0.89)</td>
<td>1.7 (48) (0.76)</td>
</tr>
</tbody>
</table>

\(^a\) Number of nests.
\(^b\) Standard deviation.

Hatching of all eggs in Sharp-shinned and Cooper’s hawk clutches occurred in 1 or 2 days. The time required for hatching of all eggs in a Goshawk clutch was not determined. Nests of each species frequently contained 1 and sometimes 2 eggs that did not hatch. Goshawks covered these with short, green fir boughs, but in Sharp-shinned and Cooper’s hawk nests, these eggs frequently remained exposed. Unhatched eggs eventually broke and the shell fragments disappeared.

The nestling period lasted 34–37 days for Goshawks, 27–30 days for Cooper’s Hawks, and 21–24 days for Sharp-shinned Hawks. Faster development of the smaller males and their subsequent earlier fledging accounted for much of the variation in length of nestling period within each species.

Mean number of Sharp-shinned Hawks fledged in Oregon was below that
Table 3

Mean Clutch Size and Number of Young Fledged per Nest of Sharp-shinned Hawk, Cooper’s Hawk, and Goshawk in this Study Compared to Others

<table>
<thead>
<tr>
<th>Species</th>
<th>Source</th>
<th>Location</th>
<th>Year</th>
<th>Clutch size</th>
<th>Number fledged/ nest attempt</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sharp-shinned Hawk</td>
<td>This study</td>
<td>Oregon</td>
<td>See Table 2</td>
<td>4.6 (5)²</td>
<td>2.7 (11)²</td>
</tr>
<tr>
<td></td>
<td>Craighead and</td>
<td></td>
<td>1947</td>
<td>3.5 (2)</td>
<td>3.5 (2)</td>
</tr>
<tr>
<td></td>
<td>Craighead, 1956</td>
<td>Wyoming</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cooper’s Hawk</td>
<td>This study</td>
<td>Oregon</td>
<td>See Table 2</td>
<td>3.8(13)</td>
<td>2.1 (24)</td>
</tr>
<tr>
<td></td>
<td>Craighead and</td>
<td></td>
<td>1942</td>
<td>4.3 (6)</td>
<td>2.0 (6)</td>
</tr>
<tr>
<td></td>
<td>Craighead, 1956</td>
<td>Michigan</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Craighead and</td>
<td></td>
<td>1948</td>
<td>4.0</td>
<td>2.3 (7)</td>
</tr>
<tr>
<td></td>
<td>Craighead, 1956</td>
<td>Michigan</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Meng, 1951</td>
<td>New York</td>
<td>1948-50</td>
<td>4.2 (36)</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>Henny and</td>
<td></td>
<td>1929-45</td>
<td>3.53 (118)</td>
<td>2.67* (54)</td>
</tr>
<tr>
<td></td>
<td>Wight, 1972</td>
<td>Northeastern U.S.</td>
<td>1949-67</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Goshawk</td>
<td>This study</td>
<td>Oregon</td>
<td>See Table 2</td>
<td>3.2 (5)</td>
<td>1.7 (48)</td>
</tr>
<tr>
<td></td>
<td>McGowan, 1975</td>
<td>Alaska</td>
<td>1971</td>
<td>3.1 (10)</td>
<td>2.5 (10)</td>
</tr>
<tr>
<td></td>
<td>McGowan, 1975</td>
<td>Alaska</td>
<td>1972</td>
<td>3.0 (14)</td>
<td>1.8 (14)</td>
</tr>
<tr>
<td></td>
<td>McGowan, 1975</td>
<td>Alaska</td>
<td>1973</td>
<td>3.8 (9)</td>
<td>1.8 (9)</td>
</tr>
<tr>
<td></td>
<td>Hakila, 1968</td>
<td>Finland</td>
<td>1955-58</td>
<td>3.4 (22)</td>
<td>1.5 (28)</td>
</tr>
<tr>
<td></td>
<td>Holstein, 1942</td>
<td>Denmark</td>
<td>1937-40</td>
<td>2.8 (9)</td>
<td>1.8 (9)</td>
</tr>
<tr>
<td></td>
<td>Hognlund, 1964</td>
<td>Fennoscandia</td>
<td>1931-40</td>
<td>3.1 (11)</td>
<td></td>
</tr>
</tbody>
</table>

² Number of nests.

*b Number of young reaching bandable age per successful nest 1929–1945.

*c Number of young reaching bandable age per successful nest 1949–1967.

reported for the same species in Wyoming in 1947 (Craighead and Craighead 1956; Table 3). Number of Cooper’s Hawks fledged per nest in Oregon was slightly above the number fledged in Michigan in 1942 and slightly below the number fledged in the same area in 1948 (Craighead and Craighead 1956; Table 3). The number of Cooper’s Hawk young fledged per successful nest in Oregon was considerably less than the number of young reaching bandable age per successful nest in the years prior to the introduction of organochlorine pesticides and slightly above the number in later years in northeastern United States—2.9 per successful nest in Oregon compared to 3.53 in 1929–1945 and 2.67 in 1949–1967 (Henny and Wight 1972; Table 3). However, since mortality between the time of banding and fledging was not determined, Henny and Wight’s (1972) figures were overestimates of productivity and not directly comparable to our data.
Table 4

Hatching Success,1 Fledging Success,2 and Percent of Total Nests of Sharp-shinned Hawks, Cooper's Hawks, and Goshawks in Oregon that Fledged at Least One Young

<table>
<thead>
<tr>
<th>Species</th>
<th>% Hatching Success</th>
<th>% Fledging Success</th>
<th>% Successful Nests</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sharp-shinned Hawk</td>
<td>69.9 (5 nests)</td>
<td>81.2 (5 nests)</td>
<td>91.7 (12 nests)</td>
</tr>
<tr>
<td></td>
<td>(23 eggs)</td>
<td>(16 young)</td>
<td></td>
</tr>
<tr>
<td>Cooper's Hawk</td>
<td>74.0 (13 nests)</td>
<td>61.4 (14 nests)</td>
<td>69.0 (29 nests)</td>
</tr>
<tr>
<td></td>
<td>(50 eggs)</td>
<td>(44 young)</td>
<td></td>
</tr>
<tr>
<td>Goshawk</td>
<td>81.2 (5 nests)</td>
<td>72.0 (11 nests)</td>
<td>90.4 (52 nests)</td>
</tr>
<tr>
<td></td>
<td>(16 eggs)</td>
<td>(25 young)</td>
<td></td>
</tr>
</tbody>
</table>

1 Number of eggs hatched/number of eggs laid.
2 Number of young fledged/number of young hatched.
3 Total number of nests.
4 Total number of eggs laid.
5 Total number of young hatched.

Number of Goshawks fledged per nest in Oregon was nearly the same as reported in southwestern Finland (Hakila 1968), Denmark (Holstein 1942), and near Fairbanks, Alaska in 1972 (McGowan 1975), but was nearly 1 young less per nest than in Alaska during 1971 (McGowan 1975; Table 3). However, mean clutch size was nearly the same for all of these locations. Similarities in clutch size in Oregon and Alaska and the relatively high fledging success in Alaska in 1971 suggested that clutch size for this species may be somewhat constant geographically and annually, while hatching and fledging success are influenced by food availability. For example, snowshoe hares (Lepus americanus) were the primary food of Goshawks in Alaska during 1970–72 (McGowan 1975). In northern latitudes hare populations are subject to an approximate 10-year population cycle (Keith 1963). In the area of Fairbanks, Alaska hare populations peaked in 1971 and decreased in numbers in 1972 through at least 1973 (McGowan 1975; J. Ernest pers. comm.). High hare density probably accounted for the high fledging success (2.5 young per nest) in 1971. In 1972, however, the number fledged per nest decreased to 1.8 young, and was again 1.8 in 1973 (McGowan 1975). In addition, the number of nests occupied in McGowan's study area was 7 in 1971, 9 in 1972, 8 in 1973, and 1 in 1974.

Age of nesting hawks.—In the North American accipiters, both sexes begin molting into adult plumage in the spring of their first year. Since this molt is not completed until the following fall, nesting accipiters can be identified as immature or adult (2 or more years old) on the basis of plumage. Of 70 Goshawk females and 10 Sharp-shinned Hawk females we observed nesting, all were in mature plumage. However, 2 females (6%) of 34 pairs of
Cooper’s Hawks were immature. Males were not observed at all of these nests, but of those seen of each species, all were in mature plumage. Meng (1951) in New York, and N. Snyder (pers. comm.) in Arizona found several immature female Cooper’s Hawks, but no immature males breeding. McGowan (1975) found 4 of 11 Goshawk females nesting in Alaska in immature plumage in 1971, while in 1972 and 1973, all were in mature plumage. He observed males at 37% of the nests, and each of these was mature. Hoglund (1964) reported that immature female Goshawks were occasionally found nesting in Finland. On the basis of an examination of testes of 10 immature male Goshawks, all of which varied in size and only 1 of which contained small amounts of mature sperm, Hoglund (1964) concluded that immature males are normally incapable of breeding. However, Glutz von Blotheim (1971) reported that 2 of 30 male (6.7%) and 9 of 93 female (9.7%) Goshawks nesting in central and southern Europe were in immature plumage.

Reynolds (1972) discussed the general lack of nesting by immature males and hypothesized that, since males are the principal food providers during the nesting season, foraging experience is a prerequisite for successful nesting. Immature males, lacking experience, may be subject to greater risks of predation or accident while foraging, and may spend greater energies in territorial establishment and defense than mature birds. Deferring the age of first breeding should increase the future fitness of an immature male. A concomitant of deferred maturity is delayed testicular growth and spermatogenesis.

Post-fledging period.—Young accipiter hawks, as the young of most birds of prey, are dependent on adults for food for some time after fledging. During the early portion of this period fledged young remain close to the nest. As flying skills develop, attachment wanes and young can be found at increasing distances, though their activity remains centered around the nest. Decreased attachment during the latter portion of this period increases the probability of overlooking fledged young when visiting a nest site. For this reason, it is difficult to determine exactly when parental care is terminated, and we report the greatest number of days (the potential length of dependency) young were found in or near the nest site after fledging.

Young of Sharp-shinned Hawks are the most inconspicuous of the 3 species and most difficult to follow once fledged. Eight days was the longest period we observed Sharp-shinned Hawks in the nest site following fledging. However, a pair in Utah, kept under surveillance by radio-telemetry, remained in the nest area for nearly a month before leaving as a family group (Platt 1973). In Oregon fledgling dependency may persist as long as 42 days for Goshawks and 53 days for Cooper’s Hawks. We concur with Ashmole and Tovar (1968) who hypothesized that extended fledgling periods in predaceous
birds occurs in species whose prey are difficult to capture, as considerable time is required for development of necessary hunting skills.

Current production trends.—To attempt a relative appraisal of production of accipiters in Oregon, we have included clutch sizes and fledging rates of accipiters from other populations (Table 3). Comparing these production figures to those from Oregon showed that, except for mean clutch size in Cooper’s Hawks and mean number of Sharp-shinned Hawks fledged per nest (discussed below), clutch size and fledging rates in Oregon are either greater than or are within the range of the figures from other populations. Of the 3 accipiters in Oregon, Sharp-shinned Hawks had the highest percentage of successful nests (91.7), although Goshawks were close behind (90.4). However, the percent of successful nests of Cooper’s Hawks was considerably lower (69.0) (Table 4), with 75% of the failures occurring in western Oregon. Causes of nest failure in Cooper’s Hawks ranged from predation upon nestlings (avian, 1 case; mammalian, 1 case), nest destruction (logging, 1 case; windstorm, 1 case), desertion of eggs (1 case) and an unexplained occurrence in which the young either died or were killed and subsequently eaten by the adults (2 cases). Causes of failure of 2 additional Cooper’s Hawk, 1 Sharp-shinned Hawk, and 2 Goshawk nests were unknown, while human disturbance caused nest desertion by the same pair of Goshawks during 2 consecutive years.

Hatching success (number of eggs hatched/number of eggs laid) was lowest for Sharp-shinned Hawks (69.6%), intermediate for Cooper’s Hawks (74.0%), and highest for Goshawks (81.2%), while fledging success (number of young fledged/number of young hatched) was highest for Sharp-shinned Hawks (81.2%), intermediate for Goshawks (72.0%), and lowest for Cooper’s Hawks (61.4%) (Table 4).

Since all nests of Sharp-shinned Hawks hatched young (the 1 unsuccessful nest failed after hatching), the low hatching success of this species resulted primarily from a high incidence of egg loss within clutches through infertility, death of embryo, and egg breakage. Each of these factors, especially egg breakage, may be related to the very high levels of pesticides in eggs reported for Sharp-shinned Hawks in Oregon (Snyder et al. 1973).

Although egg loss is an important factor reducing productivity of Cooper’s Hawks, this species suffers its greatest losses during the nestling period. Predation and the unexplained deaths of the young and subsequent consumption by the adults are the 2 most important factors reducing fledging success. Incidence of predation upon nestlings is higher for Cooper’s Hawks than either of the other accipiters in Oregon and may be related to habitat used for nesting. Nest sites of Cooper’s Hawks, particularly in western Oregon, are sufficiently open to allow the entry of large, winged predators, e.g., crows
(Corvus brachyrhynchos), ravens (C. corax), and Great Horned Owls (Bubo virginianus), while body size of Cooper's Hawks may not be sufficiently large to repel these predators.

Reproductive effort of Goshawks seems to be met with relatively high success in all 3 elements presented in Table 4. Factors decreasing the hatching success of this species are an occasional infertile or added egg, while most losses of nestlings occur within 10 days of fledging. During this period, dead young were frequently found below nests. Causes of death could not be determined. A few Goshawk eggs were collected in Oregon and analyzed for pesticides. All had relatively low levels, a fact that is consistent with the lack of any noticeable population decline in any region of North America (Snyder et al. 1973).

SUMMARY

Distribution of nests and nesting success were determined for Sharp-shinned Hawks (Accipiter striatus), Cooper's Hawks (A. cooperii), and Goshawks (A. gentilis) in western, southwestern, and eastern Oregon during 1969 through 1974. Nesting density was determined by intensively searching a 9284 ha area in western Oregon and an 11,741 ha area in eastern Oregon. These searches produced 4 Cooper's Hawk nests (1 nest/2321 ha) in 1970 and 5 nests in 1971 (1 nest/1857 ha) in western Oregon and 4 Sharp-shinned Hawk nests (1 nest/2750 ha), 5 Cooper's Hawk nests (1 nest/2200 ha), and 4 Goshawk nests (1 nest/2750 ha) in eastern Oregon. An analysis of hatching success, fledging success, and number of nests that were successful showed that Sharp-shinned Hawks suffered the greatest losses during the incubation period, and Cooper's Hawks and Goshawks during the nesting period.

ACKNOWLEDGMENTS

Collection of data on nesting accipiter hawks requires an enormous amount of man-hours. Our expectations could not have been fulfilled without the help of personnel from the U.S. Forest Service and Weyerhaeuser Company, especially G. Cornett, B. Heckel, T. Bryan, D. Williams, R. Anderson, C. Anderson, K. Horn, B. Anderson, J. Hoppe, and J. Jakabosky. Special thanks to E. Forsman, who helped with the field work from the beginning to the completion of this study. Others who helped include W. Pike, J. Tabor, and G. Lind.

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LITERATURE CITED


DEPT. OF FISHERIES AND WILDLIFE, OREGON STATE UNIV., CORVALLIS 97331. ACCEPTED 2 FEB. 1977.
SOCIAL AND FORAGING BEHAVIOR OF WARBLERS WINTERING IN PUERTO RICAN COASTAL SCRUB

WILLIAM POST

The foraging behavior and social relationships of the warblers (Parulidae) during the breeding season have been studied extensively by Morse (1967a, 1968, 1971, 1973). Parnell (1969) examined the foraging behavior of migrating warblers. Other than the studies of Eaton (1953) and Lack and Lack (1972) no work has aimed specifically at investigating the ecology of warblers wintering in the tropics. My objectives in the present study were to describe and quantify the social and foraging behavior of parulids wintering in Puerto Rican coastal scrub and where possible to compare their behavior with that reported from other regions. The Puerto Rican study sites were chosen because of the structural simplicity of the vegetation, and the relatively high density of warblers. In addition, the lack of significant predators prompted me to examine the question of what influence this might have on flocking behavior.

STUDY AREA AND METHODS

I conducted the study on El Guayacán Island (35 ha) and on La Cueva Island (20 ha) on the SW coast of Puerto Rico, 2 km SW of La Parguera. These "islands" are peninsular, connected to the mainland by a narrow mangrove forest no more than 100 m wide. Before 1960 both islands were grazed by goats. In 1962 the Puerto Rican government leased the islands to the Caribbean Primate Research Center, which uses them as sites for free-ranging rhesus macaque (Macaca mulatta) colonies. High populations of monkeys have been on the island since 1966, and foraging by monkeys has kept the vegetation stunted. Except for a few scattered trees, all vegetation is less than 3.5 m. In addition, the islands are in a severe dry zone. Rainfall is only 35 cm per year (12 yr average for La Cueva Island). Scrubby vegetation predominates: corcho (Pisonia albida), oxhorn bucida (Bucida buceras), and gumbo-limbo (Bursera simaruba) are the dominant trees. Shrubs or small trees are pigeon-berry (Bourreria suculenta), Bumelia spp., Lantana involucrata, dildo (Cephalocereus royenii), and pricklypear (Opuntia rubescens). This community type is described in detail by Gleason and Cook (1926) as the xerophytic forest of the Ponce limestone. The scrub zone is bordered by black mangrove (Avicennia nitida) and red mangrove (Rhizophora mangle).

I observed warblers between 20 December and 15 April of 1975-76. Observations were made between dawn and 09:30. I walked along narrow paths ("slow walk" of Lack and Lack 1972) and, upon encountering a warbler, noted (1) its foraging site, e.g. whether it was on a broad-leaved or narrow-leaved tree; (2) its height; (3) its position in the vertical vegetation strata, e.g. canopy or subcanopy; (4) its position in the horizontal vegetational strata—inner, middle, or outer. These parameters were recorded only once for each individual. Then, for the same bird I recorded 5 consecutive foraging tactics, e.g. leaf-gleaning, flycatching, or hovering. During the time the bird was in view, I

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also noted whether it engaged in hostile interactions, gave contact calls, and the nature of its social affiliation (alone, part of a cohesive flock, or part of a stationary flock). Total observation time was 47 h.

I conducted censuses at the same time that I made observations of foraging and social behavior. On different days than those on which I made observations, I operated mist nets (12 m long; 30 mm mesh) from dawn to 09:30, to correspond to census times. Five sites, with 5 nets at each, were used throughout the study period. Total net-hours were 153.

RESULTS AND DISCUSSION

Population composition.—Censuses and mist-netting gave the same estimates of population composition (Table 1). Only uncommon species such as Yellow-rumped Warbler and Bahama Yellowthroat were missed by either one or the other method. Differences may be explained by the fact that mist nets only cover a space from ground to 2 m. The census method is probably more accurate for conspicuous, usually canopy-feeding species such as the Cape May and Prairie warblers. The absence of Adelaide’s Warbler from the mist-net sample is explained by the fact that it was territorial, and no nets were placed within its home range. By both methods, the most common species on the study sites was the Cape May Warbler, followed by the permanent resident Yellow Warbler.

Although Lack and Lack (1972: Table 3) do not give comparative census and netting times for their Jamaica study sites, a comparison of the proportions of species seen and captured in Puerto Rico with proportions seen and captured in Jamaican lowland arid habitat shows differences. Overall they saw 34 and captured 55 individual warblers, and the numerically dominant species was Prairie Warbler (26% of those seen and 33% of those netted), followed by Ovenbird (15%, 13%), Common Yellowthroat (12%, 0), N. Parula (9%, 7%), and Palm (9%, 0). Interestingly, the ground feeding Palm Warbler and Common Yellowthroat were not represented in their net sample. The Cape May, although wintering in Jamaica, was not recorded in lowland arid habitat there.

The results of Lack and Lack’s (1972: Table 4) censuses for all 9 lowland dry limestone forest localities in Jamaica reveal a greater number of species than for my 2 Puerto Rican sites: 19 species vs. 11, although the number of individuals recorded per 10 h was almost the same: 131 in Jamaica and 129 in Puerto Rico. The total number of species of North American warblers wintering in Jamaica and Puerto Rico is the same (18; Bond 1956), and the higher number of species recorded by the Lacks is presumably due to the greater number of sites they visited. My study areas are probably most similar to the Lacks’ arid cut-over habitat, where they saw only 16 individuals of 7 warbler species per 10 h (Lack and Lack 1972: Table 5).
### Table 1

**Number of Warblers Seen and Mist-netted in Coastal Southwestern Puerto Rico**

<table>
<thead>
<tr>
<th>Species</th>
<th>El Guayacán and La Cueva study sites</th>
<th>Mainland opposite to study sites</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number seen per 10 h</td>
<td>Number captured per 100 net h</td>
</tr>
<tr>
<td>Black-and-white Warbler (Mniotilta varia)</td>
<td>4.8 (3.7)²</td>
<td>3.9 (3.5)²</td>
</tr>
<tr>
<td>Prothonotary Warbler (Protonotaria citrea)</td>
<td>1.3 (1.0)</td>
<td>2.6 (2.3)</td>
</tr>
<tr>
<td>N. Parula (Parula americana)</td>
<td>17.6 (13.7)</td>
<td>16.4 (14.8)</td>
</tr>
<tr>
<td>Yellow Warbler (Dendroica petechia)</td>
<td>18.9 (14.7)</td>
<td>19.6 (17.7)</td>
</tr>
<tr>
<td>Cape May Warbler (D. tigrina)</td>
<td>41.0 (31.9)</td>
<td>26.2 (23.7)</td>
</tr>
<tr>
<td>Black-throated Blue Warbler (D. caerulescens)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Yellow-rumped Warbler (D. coronata)</td>
<td>1.9 (1.5)</td>
<td>0</td>
</tr>
<tr>
<td>Yellow-throated Warbler (D. dominica)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Adelaide's Warbler (D. adelaidae)</td>
<td>3.5 (2.7)</td>
<td>0</td>
</tr>
<tr>
<td>Blackpoll Warbler (D. striata)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Prairie Warbler (D. discolor)</td>
<td>16.0 (12.4)</td>
<td>11.8 (10.7)</td>
</tr>
<tr>
<td>Palm Warbler (D. palmarum)</td>
<td>0</td>
<td>2.0 (1.8)</td>
</tr>
<tr>
<td>Ovenbird (Seiurus aurocapillus)</td>
<td>0</td>
<td>1.3 (1.2)</td>
</tr>
<tr>
<td>N. Waterthrush (S. noveboracensis)</td>
<td>12.7 (9.9)</td>
<td>11.8 (10.7)</td>
</tr>
<tr>
<td>Louisiana Waterthrush (S. motacilla)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Bahaman Yellowthroat (Geothlypis rostrata)</td>
<td>1.0 (0.8)</td>
<td>0</td>
</tr>
<tr>
<td>Hooded Warbler (Wilsonia citrina)</td>
<td>0</td>
<td>0.7 (0.6)</td>
</tr>
<tr>
<td>American Redstart (Setophaga ruticilla)</td>
<td>9.9 (7.7)</td>
<td>14.4 (13.0)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>128.7 (100.0)³</strong></td>
<td><strong>110.7 (100.0)³</strong></td>
</tr>
</tbody>
</table>

² Percentages in parentheses.
³ No difference between census and mist-net estimates of the relative numbers of the 8 species that were recorded by both methods ($\chi^2 = 9.6$, d.f. = 7; $0.25 > P > .1$).
Table 2
Social Affiliations of Individual Warblers Observed in Puerto Rican Coastal Scrub

<table>
<thead>
<tr>
<th>Species</th>
<th>Bird alone</th>
<th>Individuals in stationary flock*</th>
<th>Individuals in cohesive flock*</th>
<th>Total individuals in flocks*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black-and-white Warbler</td>
<td>8</td>
<td>5</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>Prothonotary Warbler</td>
<td>2</td>
<td>6</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td>N. Parula</td>
<td>15</td>
<td>55</td>
<td>5</td>
<td>76</td>
</tr>
<tr>
<td>Yellow Warbler</td>
<td>20</td>
<td>22</td>
<td>0</td>
<td>23</td>
</tr>
<tr>
<td>Cape May Warbler</td>
<td>41</td>
<td>78</td>
<td>19</td>
<td>145</td>
</tr>
<tr>
<td>Prairie Warbler</td>
<td>27</td>
<td>32</td>
<td>5</td>
<td>46</td>
</tr>
<tr>
<td>N. Waterthrush</td>
<td>24</td>
<td>3</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>American Redstart</td>
<td>13</td>
<td>19</td>
<td>0</td>
<td>29</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>150</strong></td>
<td><strong>220</strong></td>
<td><strong>31</strong></td>
<td><strong>340</strong></td>
</tr>
</tbody>
</table>

* All flocks were composed of more than 1 species.
* Includes birds that were not classified as to whether they were in stationary or cohesive flocks.

In comparison to the Christmas bird count censuses of warblers on the adjacent Puerto Rican mainland (Table 1), the results obtained on my study sites differed mainly in the higher proportion of Cape May and Prairie Warblers and lower proportion of Yellow Warblers that I recorded. Although data are lacking, these differences are presumably due to vegetational differences between the islands and adjacent mainland.

*Social behavior.*—Warblers wintering on the study sites were often members of flocks (Table 2), but these flocks were stationary aggregations, usually organized around concentrations of insects. Such flocks correspond to the “collections” of Lack and Lack (1972). The behavior of the Puerto Rican flocks was similar to that described for the Jamaican flocks: birds were often within a few meters of each other but moved about independently. The Lacks’ stationary flocks had up to 8 individuals and usually no more than 2 of 1 species. I found stationary flocks of up to 25 individuals and some species, notably Cape May and Yellow warblers, were represented by up to 7 individuals.

Few warblers, only 7.7% (31 out of 401: Table 2) were organized into cohesive flocks, i.e., flocks that maintained their integrity as they moved through the scrub. Such cohesive flocks were easily identified because their members consistently followed each other, rarely remaining at one position long.

Morse (1970) defined a flock as 2 or more birds in a group, formation of which depended upon positive responses by these individuals towards one another. Groups that form due to common responses of individuals to an extrinsic factor such as localized water or food Morse termed aggregations.
Several workers have studied stationary flocks or aggregations that gather at fruiting trees. For example, Leck (1972) described the behavior of warblers and other species aggregating at Cecropia trees in Puerto Rico. In the tropics warblers and other species often gather to forage on insects flushed by army ant swarms (Willis 1966 a,b). Flocking behavior may be viewed as an adaptation to enhance foraging efficiency (Cody 1971, Krebs et al. 1972), a means of improved protection against predators (Moynhan 1962, Powell 1974), and a means of reducing intraspecific aggression (Barash 1974). The relative importance of these factors probably varies with species and habitat. In this study I was particularly interested in flocking behavior because of the few aerial predators in the study areas. Willis (1973) correlated a widespread absence of cohesive flocks in Puerto Rico with paucity of accipiter species. The one locality where Willis found cohesive flocks, Maricao, also has Sharp-shinned Hawks (Accipiter striatus).

At the La Parguera study sites, I found 2 species of avian predators, American Kestrels (Falco sparverius) and Short-eared Owls (Asio flammeus). A pair of Kestrels lived on La Cueva in 1972–1973. In 1974 they moved to El Guayacán, probably in response to new feeding habitat created by the clearing of land. Direct observations suggested that this pair specialized on house mice (Mus musculus) and rats (Rattus norvegicus) that were abundant around monkey enclosures. Although the Kestrels flew over groups of warblers I was watching, the warblers did not appear to respond. A single Short-eared Owl appeared sporadically on El Guayacán, and it may occasionally have taken small birds, although I saw it foraging only at twilight around the monkey enclosures. On 19 February 1975 I flushed it from some dense grass, and it perched on an exposed stub, whereupon it was mobbed by a Black-and-white, a Northern Parula, a Cape May Warbler, and a Northern Waterthrush, all of which approached within 5 m of the owl. After about 3 min, the warblers resumed foraging within view of the perched owl. Cats, mongooses (Herpestes javanicus), and monkeys, all common on the study sites, did not seem to influence the behavior of foraging warblers. Twice I saw a mongoose move under foraging Northern Parulas and American Redstarts, none of which altered their behavior. Cats were active during crepuscular periods; rhesus monkeys seemed to ignore free-flying birds.

Sweep samples made at different warbler foraging sites (Table 3) revealed that insects were locally concentrated. Shrubs such as Bumelia supported abundant populations of homopterans, while neighboring patches of vegetation such as Lantana had few insects. Similarly, black mangrove stands were infested with homopterans, while adjacent red mangroves were relatively insect free. Such a patchy distribution of insects facilitated concentrations of warblers. Homopterans were so abundant that birds foraging on Bu-
### Table 3
Numbers of Arthropods Collected in February in Different Types of Vegetation in Puerto Rican Coastal Scrub and Edge

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Lantana</th>
<th>Lantana and grass (Uniola and Chloris)</th>
<th>Bumelia</th>
<th>Avicennia</th>
<th>Avicennia: Rhizophora: 90%</th>
<th>Orthoptera</th>
<th>Hemiptera and Homoptera</th>
<th>Neuroptera</th>
<th>Coleoptera</th>
<th>Lepidoptera</th>
<th>Diptera</th>
<th>Hymenoptera</th>
<th>Spiders</th>
</tr>
</thead>
<tbody>
<tr>
<td>Odonata</td>
<td>—</td>
<td>1</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>52</td>
<td>2</td>
<td>—</td>
<td>3</td>
<td>3</td>
<td>9</td>
<td>—</td>
</tr>
<tr>
<td>Orthoptera</td>
<td>—</td>
<td>7</td>
<td>6</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
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<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Hemiptera and Homoptera</td>
<td>52</td>
<td>20</td>
<td>435</td>
<td>1786(^2)</td>
<td>609(^2)</td>
<td>851</td>
<td>—</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>2</td>
<td>—</td>
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<tr>
<td>Neuroptera</td>
<td>—</td>
<td>5</td>
<td>—</td>
<td>1</td>
<td>—</td>
<td>—</td>
<td>—</td>
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<td>—</td>
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<td>—</td>
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<tr>
<td>Coleoptera</td>
<td>—</td>
<td>3</td>
<td>3</td>
<td>12</td>
<td>3</td>
<td>6</td>
<td>—</td>
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<tr>
<td>Lepidoptera</td>
<td>—</td>
<td>2</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>—</td>
<td>—</td>
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<tr>
<td>Diptera</td>
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<td>—</td>
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<td>8</td>
<td>—</td>
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<td>—</td>
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<td>—</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>—</td>
<td>35</td>
<td>44</td>
<td>—</td>
<td>1</td>
<td>7</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

\(^1\) Each sample consisted of 40 sweeps made with 35 cm net through 180° arc from ground to 3 m high. All collections made at same time of day on El Guayanán.

\(^2\) Out of 1786 homopterans, 1740 were 1 species (*Petrusa ephelis*).

\(^3\) 570 were *P. ephelis*.
melia often flushed 5–10 insects with each move. I commonly observed flocks of up to 25 warblers foraging in a dense area of Bumelia about 100 m². Although the study was conducted during the dry season (December–April), and the coastal scrub habitat has the superficial appearance of being barren, insects such as Homoptera, which can puncture plant tissue to reach phloem tissue, are abundant. Janzen (1973) commented upon the disproportionately abundant abundance of Homoptera on Caribbean islands, and he considered the numbers of Homoptera that he collected on Icacos Island, Puerto Rico (vegetationally similar to the La Parguera study sites), to be “phenomenal.” Other than birds I saw few insect predators on the study sites. Ameiva and Anolis lizards were uncommon on the study sites, although common on the adjacent mainland, and their numbers are probably reduced by cats and mongooses. I captured relatively few spiders in my sweep net samples (Table 3).

All warbler species were found most often in stationary flocks, and several were found only in stationary flocks or alone (Yellow Warbler, American Redstart, and N. Waterthrush, Table 2). The American Redstart and Northern Waterthrush, because of their foraging tactics (see below), may be predisposed to forage in one position for long periods, making them even more likely members of stationary flocks. Northern Waterthrushes occupied winter territories, as probably did Yellow Warblers, but both species apparently left them to visit insect concentrations. From the point of view of motivation, being alone or in a stationary flock may be the same, since these flocks are apparently passive assemblages. The determinants of social affiliation in these assemblages thus appeared to be food distribution and the foraging tactics of the birds.

As suggested by Cody (1971), cohesive flocking may be adaptive under conditions of low food availability. Kepler and Kepler (1970) observed that mountainous areas of Puerto Rico have fewer bird species than the lowlands and related this to the reduced number of flying insects in the mountains, perhaps due to heavy rainfall. It is significant that the only area where Willis (1973) found cohesive flocks was in the mountains, around Maricao. Willis commented upon the low productivity of Maricao, relating it to the area’s poor soil characteristics. He suggested that under the conditions of low food availability there, birds may have large home ranges, facilitating the formation of cohesive flocks. Morse (1970) demonstrated that flock-joining species showed the greatest tendency to group when overall population density was lowest, and he viewed cohesive flocking as an adaptation to improve foraging. Conversely, Morse (1967b) found that when food was abundant, Brown-headed Nuthatches (Sitta pusilla) dropped out of mixed-species flocks (of which they were usual members) to forage alone.

A possible further explanation for the lack of cohesive flocking in the
warblers I studied is the lack of nuclear species. Moynihan (1962) observed that migrants or winter visitors are joiners or followers of mixed flocks of permanent residents such as tanagers or honey creepers, which by their gregarious and conspicuous behavior act as focal points of flock integration. On my study sites no residents acted as nuclear species. Puerto Rican Todies (Todus mexicanus), although noisy, tended to remain in one area for long periods. Bananaquits (Coereba flaveola) concentrated their activities around flowers. Stolid Flycatchers (Myiarchus stolidus) foraged near groups of warblers, but their foraging method probably precluded their membership in cohesive flocks. The greater proportion of migrants which compose the avifauna of islands, e.g. 44% for Puerto Rico vs. 26% for the Canal Zone (Leck 1972) may influence the frequency of cohesive flocking, due to the relative rarity of potential nuclear species on islands.

Calling behavior.—I made 216 observations of the frequency that warblers gave contact calls, the sibilant tseep or tsip notes often heard during migration. On 99 occasions (45.8%) warblers uttered contact calls (Table 4). The occurrence of these calls was related to the social situation of the warblers. Birds in flocks gave the calls significantly more often than did those alone ($\chi^2 = 7.3$; $P < .01$), and birds in cohesive flocks called more often than those in stationary flocks ($\chi^2 = 19.6$; $P < .005$). However, birds alone and in stationary flocks called with the same frequency ($\chi^2 = 1.6$; N.S.). This latter result is further evidence of the similarity between foraging in stationary flocks and solitary foraging.

Although the data are few, some species differences in calling behavior are evident (Table 4). Cape May Warblers called proportionally more often than other species, whether alone or in flocks. At least in flocks, this could be due to the numerical dominance of this species: contact calls may be responded to more often by conspecifics. In contrast to other species, Prairie Warblers seldom called, whether in or out of flocks.

Aggressive interactions.—I recorded hostile interactions between warblers, which included chases, supplants, and fights. As found by Morse (1970), most aggressive encounters were intraspecific (Table 5). This is due to the fact that a bird is more likely to encounter a member of its own than another species in its preferred foraging space. In addition, members of the same species may be attracted by each others' morphological and behavioral characteristics (Moynihan 1962). For example, on several occasions, I saw dull-plumaged Cape Mays, presumably juveniles, following adult male Cape Mays as they foraged. Warblers that captured a large food item such as a caterpillar were often chased by conspecifics.

If we assume that each species has an equal probability of encountering another, then we may calculate the expected number of hostile interactions
<table>
<thead>
<tr>
<th>Species</th>
<th>Call given</th>
<th>No call given</th>
<th>Call given</th>
<th>No call given</th>
<th>Individuals in cohesive flocks</th>
<th>Individuals in stationary flocks</th>
<th>Total individuals in flocks</th>
</tr>
</thead>
<tbody>
<tr>
<td>N. Parula</td>
<td>0</td>
<td>0</td>
<td>10</td>
<td>0</td>
<td>16</td>
<td>0</td>
<td>19</td>
</tr>
<tr>
<td>Yellow Warbler</td>
<td>1</td>
<td>0</td>
<td>14</td>
<td>2</td>
<td>16</td>
<td>1</td>
<td>18</td>
</tr>
<tr>
<td>Cape May Warbler</td>
<td>13</td>
<td>36</td>
<td>10</td>
<td>10</td>
<td>59</td>
<td>15</td>
<td>81</td>
</tr>
<tr>
<td>Prairie Warbler</td>
<td>0</td>
<td>0</td>
<td>11</td>
<td>3</td>
<td>18</td>
<td>0</td>
<td>20</td>
</tr>
<tr>
<td>American Redstart</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>15</td>
<td>36</td>
<td>76</td>
<td>22</td>
<td>84</td>
<td>3</td>
<td>81</td>
</tr>
</tbody>
</table>

*Includes birds that were not classified as to whether they were in stationary or cohesive flocks.*
Table 5
HOSTILE INTERACTIONS OF WARBLERS WINTERING IN PUERTO RICAN COASTAL SCRUB

<table>
<thead>
<tr>
<th>Species attacking</th>
<th>Prothonotary Warbler</th>
<th>N. Parula</th>
<th>Yellow Warbler</th>
<th>Cape May Warbler</th>
<th>Prairie Warbler</th>
<th>N. Waterthrush</th>
<th>American Redstart</th>
<th>Unidentified Warbler</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prothonotary Warbler (14.1;12.7-15.5)(^1)</td>
<td>—</td>
<td>—</td>
<td>1</td>
<td>1</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>N. Parula (7.5 ± 0.3)(^2)</td>
<td>—(0)(^3)</td>
<td>3(1)</td>
<td>—(1)</td>
<td>1(3)</td>
<td>1(1)</td>
<td>—(1)</td>
<td>—(1)</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td>Yellow Warbler (11.3 ± 0.5)</td>
<td>—(0)</td>
<td>—(2)</td>
<td>2(2)</td>
<td>6(4)</td>
<td>—(1)</td>
<td>1(1)</td>
<td>1(1)</td>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td>Cape May Warbler (10.1 ± 0.2)</td>
<td>—(1)</td>
<td>13(9)</td>
<td>—(10)</td>
<td>44(22)</td>
<td>2(8)</td>
<td>—(6)</td>
<td>—(5)</td>
<td>1</td>
<td>60</td>
</tr>
<tr>
<td>Prairie Warbler (6.9 ± 0.2)</td>
<td>—(0)</td>
<td>1(1)</td>
<td>—(1)</td>
<td>—(2)</td>
<td>4(1)</td>
<td>—(1)</td>
<td>—(0)</td>
<td>—</td>
<td>5</td>
</tr>
<tr>
<td>N. Waterthrush (15.1 ± 0.6)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>1</td>
<td>—</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>American Redstart (7.4 ± 0.3)</td>
<td>1</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>2</td>
<td>—</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Unidentified Warbler</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>1</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>Total</td>
<td>1</td>
<td>17</td>
<td>3</td>
<td>53</td>
<td>7</td>
<td>1</td>
<td>4</td>
<td>11</td>
<td>97</td>
</tr>
</tbody>
</table>

\(^1\) Mean weight (g) followed by range (N = 5).
\(^2\) Mean weight (g) followed by 95% confidence interval (sample size >10) for species other than Prothonotary Warbler.
\(^3\) Expected number of aggressive encounters, correcting for relative abundance (Table 1) and assuming all species are equally likely to encounter each other (for species which gave 5 or more attacks to identified species).

per species pair (Table 5: values in parentheses). A comparison of observed and expected values shows that birds did attack members of their own species more often than expected. The Cape May, which comprised 32% of the warbler population (Table 1) gave 62% of the attacks (Table 5), and 73% of these were to conspecifics. Species which were similar in foraging behavior were also attacked more frequently than expected; for example Cape Mays vs. Parulas. The 4 species for which I have sufficient data may be ordered into a linear hierarchy with Yellow Warblers dominating Cape Mays, fol-
<table>
<thead>
<tr>
<th>Species</th>
<th>Number of observations</th>
<th>Mean</th>
<th>95% Confidence interval</th>
<th>Distribution of birds at different heights (m above ground)</th>
<th>Distribution of birds in vertical structural units of vegetation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Number of observations</td>
<td>Percentage at:</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0-1</td>
<td>1-2</td>
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<tr>
<td>Black-and-white Warbler</td>
<td>22</td>
<td>1.39</td>
<td>±0.25</td>
<td>22</td>
<td>22.7</td>
</tr>
<tr>
<td>Prothonotary Warbler</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>13</td>
<td>38.5</td>
</tr>
<tr>
<td>N. Parula</td>
<td>101</td>
<td>2.47</td>
<td>±0.30</td>
<td>107</td>
<td>7.5</td>
</tr>
<tr>
<td>Yellow Warbler</td>
<td>51</td>
<td>1.89</td>
<td>±0.32</td>
<td>53</td>
<td>11.3</td>
</tr>
<tr>
<td>Cape May Warbler</td>
<td>183</td>
<td>2.82</td>
<td>±0.30</td>
<td>230</td>
<td>15.2</td>
</tr>
<tr>
<td>Prairie Warbler</td>
<td>84</td>
<td>2.12</td>
<td>±0.26</td>
<td>87</td>
<td>17.2</td>
</tr>
<tr>
<td>N. Waterthrush</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>28</td>
<td>96.4</td>
</tr>
<tr>
<td>American Restart</td>
<td>44</td>
<td>1.57</td>
<td>±0.20</td>
<td>48</td>
<td>29.2</td>
</tr>
<tr>
<td>Species</td>
<td>Number of observations</td>
<td>Broad-leaved vegetation</td>
<td>Dead vegetation</td>
<td>Narrow-leaved vegetation</td>
<td>Herbs and succulents</td>
</tr>
<tr>
<td>------------------------</td>
<td>------------------------</td>
<td>-------------------------</td>
<td>-----------------</td>
<td>--------------------------</td>
<td>----------------------</td>
</tr>
<tr>
<td>Black-and-white Warbler</td>
<td>22</td>
<td>86.4</td>
<td>13.6</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Prothonotary Warbler</td>
<td>12</td>
<td>58.3</td>
<td>-</td>
<td>16.7</td>
<td>25.0</td>
</tr>
<tr>
<td>N. Parula</td>
<td>105</td>
<td>81.0</td>
<td>5.7</td>
<td>5.7</td>
<td>6.7</td>
</tr>
<tr>
<td>Yellow Warbler</td>
<td>56</td>
<td>73.2</td>
<td>7.1</td>
<td>14.3</td>
<td>3.6</td>
</tr>
<tr>
<td>Cape May Warbler</td>
<td>216</td>
<td>62.0</td>
<td>13.0</td>
<td>11.6</td>
<td>10.6</td>
</tr>
<tr>
<td>Prairie Warbler</td>
<td>89</td>
<td>56.2</td>
<td>9.0</td>
<td>18.0</td>
<td>12.3</td>
</tr>
<tr>
<td>N. Waterthrush</td>
<td>31</td>
<td>16.1</td>
<td>-</td>
<td>-</td>
<td>6.5</td>
</tr>
<tr>
<td>American Redstart</td>
<td>45</td>
<td>88.9</td>
<td>-</td>
<td>11.1</td>
<td>-</td>
</tr>
</tbody>
</table>
followed by Northern Parulas, then Prairies. This is also the order of decreasing weight (Table 5).

Foraging behavior.—My observations indicate that warblers wintering in Puerto Rican coastal scrub often used similar foraging spaces and feeding tactics (Table 6–9). Two species, the Black-and-white Warbler, a trunk and branch gleaner, and the Northern Waterthrush, a ground feeder, are clearly separated from the other species. Of the others, all of which concentrated their foraging activities in above-ground foliage, the American Redstart is a specialist of the inner subcanopy (Table 8), and it obtained most of its prey on the wing (Table 9). The remaining 4 species, the Northern Parula, Yellow, Cape May, and Prairie warblers were not clearly separated in their foraging behavior: The similarities among these species may be quantified by using the index of overlap (Table 10) developed by Horn (1966):

\[ R_0 = \frac{\sum (x_i + y_i) \log (x_i + y_i) - \sum x_i \log x_i - \sum y_i \log y_i}{(X + Y) \log (X + Y) - X \log X - Y \log Y}, \]

where \( X \) and \( Y \) equal the number of observations in samples of foraging of the two species being compared; \( x_i \) and \( y_i \) equal the proportion of observations in the \( i^{th} \) foraging category of the samples.

The data show broad overlap in many categories of foraging behavior, particularly in foraging site use and in foraging tactics. Less overlap was shown among use of structural units. Northern Parulas were very similar to Cape Mays in the 3 parameters considered. Parulas were also somewhat close to Prairies but quite dissimilar to American Redstarts. The Cape May overlapped broadly in at least 2 categories with each of the other 4 species and, after the N. Parula, was most similar to the Prairie. The Yellow Warbler was closest to the Prairie Warbler.
### Table 9

**Foraging Tactics of Warblers in Puerto Rican Coastal Scrub**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Observations</th>
<th>Leaf gleaning</th>
<th>Trunk or branch gleaning</th>
<th>Twig gleaning</th>
<th>Fly-catching</th>
<th>Hovering</th>
<th>Fruit eating</th>
<th>Chasing</th>
<th>Web feeding</th>
<th>Nectar feeding</th>
<th>Ground pecking</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black-and-white Warbler</td>
<td>85</td>
<td>11.8</td>
<td>75.3</td>
<td>5.9</td>
<td>4.7</td>
<td>2.4</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Prothonotary Warbler</td>
<td>41</td>
<td>41.5</td>
<td>9.8</td>
<td>43.9</td>
<td>4.9</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>N. Parula</td>
<td>335</td>
<td>70.1</td>
<td>2.1</td>
<td>6.9</td>
<td>9.5</td>
<td>4.8</td>
<td>-</td>
<td>2.4</td>
<td>0.3</td>
<td>3.9</td>
<td>-</td>
</tr>
<tr>
<td>Yellow Warbler</td>
<td>114</td>
<td>57.0</td>
<td>4.4</td>
<td>15.8</td>
<td>10.5</td>
<td>7.9</td>
<td>-</td>
<td>-</td>
<td>3.5</td>
<td>0.9</td>
<td>-</td>
</tr>
<tr>
<td>Cape May Warbler</td>
<td>553</td>
<td>40.1</td>
<td>3.9</td>
<td>9.5</td>
<td>28.0</td>
<td>3.8</td>
<td>4.3</td>
<td>2.0</td>
<td>2.3</td>
<td>5.2</td>
<td>0.9</td>
</tr>
<tr>
<td>Adelaide's Warbler</td>
<td>18</td>
<td>50.0</td>
<td>11.1</td>
<td>-</td>
<td>22.2</td>
<td>16.7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Prairie Warbler</td>
<td>216</td>
<td>36.1</td>
<td>1.8</td>
<td>26.4</td>
<td>16.7</td>
<td>8.8</td>
<td>-</td>
<td>7.4</td>
<td>0.5</td>
<td>1.8</td>
<td>0.5</td>
</tr>
<tr>
<td>N. Waterthrush</td>
<td>18</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>5.6</td>
<td>5.6</td>
<td>-</td>
<td>22.2</td>
<td>-</td>
<td>-</td>
<td>61.1</td>
</tr>
<tr>
<td>American Redstart</td>
<td>153</td>
<td>8.2</td>
<td>0.6</td>
<td>3.2</td>
<td>45.6</td>
<td>29.8</td>
<td>-</td>
<td>11.4</td>
<td>0.6</td>
<td>-</td>
<td>0.6</td>
</tr>
</tbody>
</table>

1. Structures less than 10 mm in diameter classified as twigs.
2. A bird engaged in chasing when it fluttered or ran along a horizontal surface in pursuit of prey.
3. Web-feeding birds reached out to take spiders or spiders' prey from web or thread.
<table>
<thead>
<tr>
<th>Species</th>
<th>Yellow Warbler</th>
<th>Cape May Warbler</th>
<th>Prairie Warbler</th>
<th>American Redstart</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Foraging sites</td>
<td>Structural units</td>
<td>Foraging tactics</td>
<td>Foraging sites</td>
</tr>
<tr>
<td>N. Parula</td>
<td>0.98</td>
<td>0.87</td>
<td>0.98</td>
<td>0.97</td>
</tr>
<tr>
<td>Yellow Warbler</td>
<td>0.98</td>
<td>0.79</td>
<td>0.89</td>
<td>0.99</td>
</tr>
<tr>
<td>Cape May</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Warbler</td>
<td>0.99</td>
<td>0.72</td>
<td>0.91</td>
<td></td>
</tr>
<tr>
<td>Prairie Warbler</td>
<td>0.84</td>
<td>0.70</td>
<td>0.75</td>
<td></td>
</tr>
</tbody>
</table>
Lack and Lack (1972) presented data on the foraging behavior of warblers wintering in Jamaica. Unfortunately, they lumped data from different habitats and localities, so it is not possible to quantify the overlap of feeding behavior with confidence. They stated that most of their flocks were collections, i.e., stationary flocks, perhaps attracted to locally abundant food, and this implies that within habitats there could have been much overlap among species. For example, 2 species in Jamaica that were not separated by habitat, Cape May and N. Parula, were said to be separated by feeding sites and foraging heights (Lack and Lack 1973: Table 11). These are roughly equivalent to my foraging sites (Table 7) and foraging heights (Table 6). The foraging site overlap value for these 2 species in Jamaica was 0.98 vs. my value of 0.97. In Jamaica the mean foraging height for these 2 did not differ significantly (N. Parula:6.4 m; 95% confidence interval ±0.6 m; Cape May:7.6 ±1.1 m). Comparable heights in Puerto Rico were N. Parula:2.5 ±0.3 m; Cape May:2.8 ±0.3 m. In Jamaica, Prairie Warblers and N. Parula Warblers were also not separated by habitat, and their feeding site overlap is 0.99 (vs. 0.94 in Puerto Rico), while their feeding heights are not significantly different (N. Parula:6.4 ±0.6 m; Prairie:5.3 ±0.8 m vs. Puerto Rican figures of 2.5 ±0.3 and 2.1 ±0.3). My data indicate that there is less overlap among species in the structurally simple Puerto Rican habitat than in Jamaica. However, the Jamaican data are from several habitats and sites and thus may show more overlap due to the lumping of different data sets.

The patches of food visited by the stationary flocks that I studied were composed mainly of 1 species of insect (Table 3). Morse (1970) noted a convergence in the foraging behavior and use of feeding site of Brown-headed Nuthatches and Pine Warblers (Dendroica pinus) as they exploited heavy crops of pine seeds, even though this resulted in increased numbers of aggressive encounters.

When food is locally abundant and accessible, there may be little pressure for feeding specialization by members of mixed flocks. Food may be obtained by the simplest method, and if birds are using the same prey, convergence in their foraging patterns would be expected. North American warblers wintering in localities with high food concentrations appear to show few behavioral differences when foraging. As Willis (1966a) pointed out, superabundance of food may be frequent rather than exceptional due to the "irregularity principle": available food is often left by irregularities in time or space, since resource exploitation lags behind its appearance. In the tropics North American migrants, because of their mobility and opportunistic behavior, may often concentrate on irregularly distributed food that is not effectively used by resident populations.
SUMMARY

The population density of warblers wintering in arid coastal scrub in Puerto Rico was much higher than comparable sites in Jamaica. Warblers wintering in the coastal scrub usually foraged alone or in stationary (passive) flocks. Few were organized into cohesive (integrated) flocks. Warblers in stationary flocks gave contact calls with the same frequency as those alone, while warblers in cohesive flocks called more often. Aggressive behavior was common, and occurred most often between members of the same species or those with similar foraging behavior. The stationary flocks were usually composed of birds that gathered to harvest concentrations of insects whose distribution varied between vegetation patches. The few predators in the study sites apparently did not influence the flocking behavior of the warblers. Warblers showed considerable overlap in their feeding behavior, which may be due to convergence of foraging on the same abundant food source.

ACKNOWLEDGMENTS

I thank the Caribbean Primate Research Center for allowing access to El Guayacán and La Cueva. Dr. David Stephan, N. C. State University, kindly identified homopterans.

LITERATURE CITED


DDE RESIDUES AND EGGSHELL THINNING IN LOGGERHEAD SHRIKES

WILLIAM L. ANDERSON AND RONALD E. DUZAN

Relationships among high DDE concentrations, eggshell thinning, and population declines in birds have received much attention in recent years (Ratcliffe 1970, Anderson and Hickey 1972, Cooke 1973, Stickel 1975). Most severely affected are bird- and fish-eating species of Falconiformes and Pelecaniformes. DDE, a metabolite of DDT, apparently interferes with deposition of calcium carbonate in the shell gland, with consequences manifested as thinned eggshells, increased egg breakage, and production of few young.

In this paper we present evidence that the Loggerhead Shrike (Lanius ludovicianus) has suffered much the same fate as many of the large predators and that the causative agent is possibly p,p'-DDE. Shrike populations have declined in much of the Midwest (Mayfield 1949, Petersen 1965, Erdman 1970, Graber et al. 1973). Graber et al (1973:7-8) concluded that "there apparently were two levels of change in the shrike population of northern and central Illinois—a relatively slow decline since about 1900, probably related to the removal of hedges in many areas, and a very rapid decline to near zero between 1957 and 1965 from causes unknown. It is possible, of course, that this change is temporary, but as of 1972 we have seen no sign of recovery by the shrike population." Erdman (1970:150) speculated that the decline of this passerine in Wisconsin was caused by pesticides.

METHODS

We conducted our study on low-density populations (mean of 7.4 shrikes counted per day of driving in April) of Loggerhead Shrikes in southern Illinois (15 counties south of Cumberland County) in 1971 and 1972. Sixty-nine birds were collected during 4 periods of the year—January, April, July, and September. Twenty clutches (104 eggs) that we considered complete were collected in April and May. After being weighed, each egg was opened by cutting the shell along the long axis. Samples of fat (subcutaneous and visceral combined) were excised from the birds and, along with the entire contents of the eggs, were saved for analysis.

The length and breadth of eggs were estimated to the nearest 0.01 mm with a vernier dial caliper graduated in 0.05-mm intervals. The air-dried shells were weighed to the nearest 1 mg. Mean thickness of each shell with membrane attached was estimated to the nearest 1 \( \mu \) by taking 6 measurements (2 each at the large end, small end, and equator) with a micrometer graduated in 0.01-mm intervals. The same techniques were used to determine the length, breadth, and weight of 36 shrike eggs examined in the Chicago Museum of Natural History. However, measurements for 49 eggs in other archival collections were made to the nearest 0.05 mm and 10 mg. Museum eggs were used only if their blow holes were \( \leq 2 \) mm and if they were taken from "complete" clutches in southern Illinois prior to 1940.

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Sixteen shrike nests found in 1972 were not disturbed. Each was revisited at 3- to 7-day intervals to determine the rate of survival of nests and eggs, and the number of fledglings produced per successful clutch.

Samples of fat and egg contents were saponified in a KOH-ethanol solution, put through a florisil column and, if not sufficiently cleaned, subjected to acetonitrile partitioning. The samples were then analyzed for p,p’-DDE, dieldrin, and heptachlor epoxide with a Beckman model GC-4 gas chromatograph equipped with an electron capture detector. Columns were packed with 1% EPON 1001 resin and 0.5% Viton A fluoroelastomer on a solid support of 100-120 mesh Chromosorb W. The column was operated at 190°C with ultra-pure helium as the carrier gas flowing at about 45 cc per min; the detector temperature was 250°C. The lower limit of detection was considered to be 0.01 ppm on a wet-weight basis; recovery was 90%.

Statistical tests used in this study are analysis of variance and linear correlation (Snedecor 1956:160, 268-270).

RESULTS

Pesticide concentrations.—Detectable concentrations of p,p’-DDE (hereafter called “DDE”) were present in fat of 88% of the 69 Loggerhead Shrikes examined. The frequency of occurrence was 93% for 30 adult females, 86% for 28 adult males, and 82% for 11 juveniles. Mean concentrations of DDE were 21.89 ± 3.11 ppm (median = 13.88 ppm) for all birds, 19.33 ± 3.44 ppm for adult females, 27.85 ± 6.41 ppm for adult males, and 13.96 ± 3.90 ppm for juveniles.

Shrikes collected in April and July—i.e., local breeders and their young—contained greater concentrations of DDE than did shrikes collected in Sep-
Table 2

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>1875–1895</th>
<th>1971–1972</th>
<th>F Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) Length (mm)</td>
<td>24.72 ± 0.11(84)$^1$</td>
<td>24.95 ± 0.11(61)</td>
<td>2.14</td>
</tr>
<tr>
<td>(2) Breadth (mm)</td>
<td>18.67 ± 0.04(85)</td>
<td>18.52 ± 0.07(61)</td>
<td>3.53</td>
</tr>
<tr>
<td>(3) Weight (mg)</td>
<td>251 ± 2(83)</td>
<td>244 ± 2(98)</td>
<td>2.79</td>
</tr>
<tr>
<td>(4) Size Index (1) × (2)</td>
<td>451 ± 2(84)</td>
<td>462 ± 3(61)</td>
<td>0.03</td>
</tr>
<tr>
<td>(5) Thickness Index (3)/(4)</td>
<td>0.544 ± 0.003(83)</td>
<td>0.530 ± 0.005(57)</td>
<td>6.61$^2$</td>
</tr>
<tr>
<td>(6) Thickness (μ)</td>
<td>—</td>
<td>92 ± 0.4(95)</td>
<td></td>
</tr>
<tr>
<td>(7) Weight of whole egg (g)</td>
<td>—</td>
<td>4.25 ± 0.05(104)</td>
<td></td>
</tr>
<tr>
<td>(8) DDE (ppm)$^3$</td>
<td>—</td>
<td>3.09 ± 0.09(104)</td>
<td></td>
</tr>
</tbody>
</table>

$^1$Number of eggs.
$^2$Significant (P < 0.05).
$^3$Median = 1.79, range = 0.48–34.14.

tember and January (Table 1). The difference between the means for adult males was significant (P < 0.05).

The contents of the 104 eggs analyzed contained a mean concentration of 3.09 ppm of DDE (Table 2). A clutch of 6 eggs collected in 1971 had a mean of 17 ppm, with 1 egg containing a high of 34 ppm. Dieldrin and heptachlor epoxide were not detected in the eggs or the samples of fat.

Physical characteristics of eggs.—The mean value for the shell thickness index was 2.57% less for shrike eggs collected in 1971 and 1972 than for eggs of this species collected between 1875 and 1895 (Table 2). This difference was significant (P < 0.05). Mean values for other physical characteristics—length, breadth, weight, and size index—did not differ significantly between the recently collected and older eggs.

Linear correlation indicated that a negative relationship existed between concentrations of DDE and the thickness of shells for the recent eggs: $\hat{Y} = 92.610 - 2.412 \log_{10} X$, $r = -0.208$ with 93 df (P < 0.05). Correlations between concentrations of DDE and other physical characteristics were not significant.

Rothstein (1972) found that the number of eggs in the clutch and the degree of embryonic development influenced eggshell thickness in Cedar Waxwings (Bombycilla cedrorum). This was not true of the shrike eggs collected in 1971 and 1972. In clutches with ≤5 eggs, mean ± SE eggshell thickness was 92.4 ± 0.8 μ for 17 eggs without development and 94.0 ± 1.5 μ for 4 eggs with development. In clutches of 6–7 eggs, mean thickness was 89.9 ± 6
μ for 12 eggs without development and 92.0 ± 0.5 μ for 57 eggs with development. None of the differences among these means was significant (F = 1.86 with 3 and 86 df).

Nest success.—As determined by Mayfield’s (1961) day exposure method, survival of nests studied in 1972 was 79% during incubation (n = 13), 91% during the nestling period (n = 13), and 72% from start of incubation to fledging. Survival of eggs was 75% during incubation (n = 74) and 83% during the period of hatching (n = 54). Survival of young during the nestling period was 88% (n = 57). Thus, 55% of the eggs present at the beginning of incubation produced young that eventually fledged. A mean of 3.9 young fledged per successful nest (n = 9).

DISCUSSION

Data obtained during this study strongly suggest that Loggerhead Shrikes in Illinois have acquired appreciable amounts of DDE and that eggshell thickness has been adversely affected. However, the shrikes were not as severely contaminated with DDE as some raptorial and piscivorous species—birds well known for the eggshell thinning syndrome, poor reproductive success, and population declines. For example, mean concentrations (wet-weight basis) in Peregrines (Falco peregrinus) in Alaska were 38.2 ppm in fat of juveniles, 622.0 ppm in fat of adults, and 12.48 ppm in eggs (Cade et al. 1968: 175). Mean concentrations in eggs from North America and western Europe were 8.6 ppm for 16 species of Falconiformes and 17.7 ppm for 5 species of Pelecaniformes, as calculated from data presented by Stickel (1973:260–267).

The shrike’s high position in the food pyramid is almost certainly the overriding factor leading to DDE accumulation in the species. The recent finding by Graber et al. (1973:12), who examined stomachs of the birds we analyzed for pesticides, that shrikes frequently consume ground beetles (Carabidae) is particularly relevant. Because of the predaceous habits of these insects, they themselves might be expected to accumulate pesticides, which would be passed on to shrikes and other predators that feed on the beetles.

The relationship between eggshell thinning and high DDE concentrations in shrikes parallels the well-documented eggshell thinning syndrome in the Peregrine, Bald Eagle (Haliaeetus leucocephalus), Brown Pelican (Pelecanus occidentalis), and certain other birds (Ratcliffe 1970, Anderson and Hickey 1972, Faber and Hickey 1973, Blus 1974). Like these species, the eggshell thinning in shrikes occurred concurrently with declining or reduced populations. However, our data on nesting success reveal that shrikes were highly successful in producing fledglings in the low-density population in southern Illinois in 1972. Graber et al. (1973:9) reported similar findings for shrikes in central Illinois in 1958–64 (population now extirpated) and in south-
eastern Illinois in 1967. Broken eggs, crushed embryos, or other indications of atypical egg mortality were not detected (Richard R. Graber, pers. comm.).

We conclude that the factor or factors that caused the decline of the Loggerhead Shrike population in Illinois were more closely associated with survival of fledged juveniles or adults than with reproduction. We have not demonstrated that the causative factor was DDE. Nevertheless, suspicion can be directed toward this environmental toxicant because (1) it has contaminated the shrike population and (2) a relationship exists between it and the malfunction of at least 1 physiological process—eggshell thickness—in the species.

SUMMARY

Investigations in southern Illinois in 1971 and 1972 suggest that the Loggerhead Shrike has been contaminated with DDE and that the species has experienced eggshell thinning. Mean concentrations of DDE were 21.89 ppm in fat of 69 birds and 3.09 ppm in the contents of 104 eggs. A negative correlation was found between concentrations of DDE and eggshell thickness, and the mean value for the shell thickness index was 2.57% less for eggs collected during the study than for eggs in archival collections. However, nesting success was high, suggesting that the factor—DDE or other—causing the recent decline of the shrike population in Illinois was more closely associated with survival of fledged juveniles or adults than with reproduction.

ACKNOWLEDGMENTS

Appreciation is extended to the following personnel of the Illinois Natural History Survey: to J. W. Seets for assistance in collecting shrikes, locating nests, and dissecting specimens; to G. C. Sanderson and H. C. Schultz for editorial help; and to R. R. Graber for critically reading the manuscript. E. E. Klaas, Patuxent Wildlife Research Center, Laurel, Maryland, kindly provided measurement data on eggs in archival collections.

LITERATURE CITED


SECTION OF WILDLIFE RESEARCH, ILLINOIS NATURAL HISTORY SURVEY, URBANA 61801 (PRESENT ADDRESS WLA: DIVISION OF WILDLIFE RESOURCES, ILLINOIS DEPT. OF CONSERVATION, SPRINGFIELD 62701.) ACCEPTED 10 JAN. 1977.
TREE SPECIES USED BY BIRDS IN LOGGED AND UNLOGGED MIXED-CONIFEROUS FORESTS

KATHLEEN E. FRANZREB

A number of studies have examined the possible ways birds use their habitat to permit optimum exploitation and to allow coexistence of different species. Habitat partitioning may occur if, for example, each species possesses a characteristic foraging height distribution (Hartley 1953, Morse 1968, Diamond 1973). Birds may also divide the vegetation into various horizontal levels (Colquhoun and Morley 1943, MacArthur 1964, Balda 1969). Individuals of a given species may also primarily restrict their activities to specified zones in the tree such as the trunk or outer branches (Hartley 1953, MacArthur 1958, Morse 1967a, 1967b, Stallcup 1968, Sturman 1968, Koch et al. 1970). There is evidence that some avian species do have preferences for certain plant species (Hartley 1953, Morse 1967b, Balda 1969, Willson 1970, Jackson 1970, Austin and Smith 1972). These factors by acting individually or in concert may interact to produce habitat partitioning for the various avian species in the community.

It has been suggested that plant species diversity has little effect on a community’s bird species diversity which instead, is dependent upon foliage height diversity, at least in homogeneous environments (MacArthur and MacArthur 1961). It is the vegetation profile which determines bird species diversity and not the number of plant species present. Yet, the nature of the vegetation may be important in a heterogeneous environment. MacArthur (1964) found that in the complex environment of the Chiricahua Mountains, Arizona, birds “apparently used more than just profile in selecting suitable habitats; presumably the addition of nest holes and water, the change from oak to pine and from sparse to dense foliage, all made significant changes in the acceptability of the habitat for many species.” It appears that birds do not regard all trees of the same height and profile, belonging to different species, as being equally desirable for activities such as foraging and nesting.

The purpose of this investigation was to determine if birds select certain tree species in a mixed-coniferous forest, and if so, to what extent the use of a logged area differs from that of a virgin forest. Results from this study may suggest some guidelines for future timber harvesting practices in the Southwest.

STUDY AREA AND METHODS

Study area.—The study site was located on the Willow Creek watershed (202 ha logged; 131 ha unlogged), approximately 80 km south of Springerville on the Apache-Sitgreaves
National Forest, Greenlee Co., White Mountains, Arizona. It is a U.S. Forest Service experimental watershed ranging in elevation from 2682 to 2804 m.

Vegetation.—Sampling of trees with dbh (diameter at breast height) ≥7.6 cm in the unlogged and lumbered areas was conducted using the pointless point-quarter method (Cottam and Curtis 1956). One-hundred stations (400 trees) were sampled in a 15.5 ha study plot in each area. For the tree in each quadrat closest to the center stake, the following data were taken: tree species; tree height; dbh; and distance from the center of the trunk to the stake. Quaking aspen (Populus tremuloides) and snags (dead trees) had not been removed when part of the watershed was logged in the summer of 1972.

Foliage volume.—Use of the available live foliage volume was analyzed by estimating the amount of foliage for each tree species in the modified and unaltered habitats. Data for these analyses were collected simultaneously with those of the point-quarter measurements. Tree species, tree height, height to the first live branch, length of the longest branch, and distance from the center of the trunk to the first live foliage on the longest branch were recorded for each tree sampled.

An estimate of live foliage present for a given tree species was determined by calculating the total amount of foliage for each tree and then subtracting from this the value of the dead volume (the inner area of the tree which was devoid of live needles or leaves). To obtain volume in terms of m$^3$/ha for a particular tree species, I divided the live volume for each species by the number of trees of the given species sampled. Next, I multiplied this by the absolute density of the species sampled. The result is live foliage volume (m$^3$/ha) of the given tree species.

The actual formulae used to estimate volumes for a given tree were:

$$\text{Live foliage volume for spruces (Picea spp.), firs (Abies spp.), and Douglas-fir (Pseudotsuga menziesii)} = \frac{\pi}{3} (r_0^2 h_0 - r_1^2 h_1)$$
$$\text{where } h_1 = h_0 - (r_0 - r_1)$$

$$\text{Live foliage volume for pines (Pinus spp.)} = \pi (r_0^2 h_0 - r_1^2 h_1)$$
$$\text{where } h_1 = h_0 - (r_0 - r_1)$$

$$\text{Live foliage volume for quaking aspen} = \frac{4}{3} \pi (r_0^3 - r_1^3)$$

In all cases, $r_0$ represents the length of the longest branch and $r_1$ is the distance from the center of the trunk to the beginning of the live vegetation on the longest branch. $h_0$ represents the height of the tree’s live vegetation (i.e., total tree height—height to first branch). $h_1$ is the height of the portion of the tree containing branches which have dead foliage, minus the height to the first branch.

Avian tree species selection.—When a bird was observed in a tree, the following data were recorded: bird species, tree species, and activity (singing, foraging, observing, or resting). Data were collected at all daylight hours throughout the summers of 1973 and 1974 by systematically traversing the study plots along established parallel transect lines. One observation per bird was recorded and the number of such observations is indicated by N. I obtained 4868 total observations in the unharvested site and 4964 in the modified habitat.

Preferences for certain tree species were noted by comparing frequency of use of a particular tree species with its percent availability in the habitat as calculated from foliage volume data. Relative density of snags as determined from point-quarter data was used for comparative purposes as no foliage was found on them.

Data were analyzed separately for the Yellow-bellied Sapsucker (Sphyrapicus varius), Mountain Chickadee (Parus gambeli), Ruby-crowned Kinglet (Regulus calendula), Yellow-rumped Warbler (Dendroica coronata), and Gray-headed Junco (Junco caniceps). These 5 species were selected because they are representative of hole, open-cup, and ground nesting species and because they were present in sufficient densities in both.
habitats to afford adequate sample sizes. Data for the entire avifauna included these as well as all other species. Niche breadth was calculated for each species using the following formula (Shannon 1948): \[ B = - \sum p_i \ln p_i \] where B is the habitat niche breadth and \( p_i \) is the proportion of observations occurring in the \( i^{th} \) tree species.

**Avian densities.**—Species densities were determined using the spot-map method (Williams 1936) whereby a 15.5 ha grid pattern was established in the unlogged and harvested areas using plastic flagging placed at 25 m intervals along 9 parallel lines, each 390 m in length, and 50 m apart. I labelled each flag with a number corresponding to the transect line and a letter corresponding to the distance traveled from the beginning of the line. Censusing was conducted 6 times per month (June, July, and August) in each habitat.

**RESULTS**

**Vegetation.**—In the unharvested area total tree density was 626.2 trees per ha versus 167.7 in the harvested site (Table 1). In both habitats, Douglas-fir had the highest density as well as the highest importance value. In the logged area snags and quaking aspen, neither of which were removed during logging, were of considerable importance. The category "snags" contained representatives of every tree species.

**Foliage volume.**—Ponderosa pine (Pinus ponderosa) (35.9%) , followed closely by southwestern white pine (Pinus strobiformis) (35.3%) , and Douglas-fir (17.6%) had the greatest foliage volume in the unharvested site (Table 1). However, in the logged habitat quaking aspen contained the majority of total foliage volume available (53.1%). Southwestern white pine (12.6%) and Douglas-fir (11.0%) comprised considerably less foliage volume than did aspen.

**Avian tree species selection.**—I used Neyman's (1949) statistical test to evaluate differences between actual avian tree species use and the expected number of observations based upon the foliage volume availability of the various tree species. The following results were all statistically significant at the \( P \leq 0.05 \) level unless otherwise indicated.

Tree species preferences for the entire avifauna in the unaltered site (Fig. 1) indicated significant preferences for Douglas-fir, white fir (Abies concolor), and Engelmann spruce (Picea engelmanni). However, certain tree types were not used to the extent to which they were available such as ponderosa pine, southwestern white pine, and snags. There was no significant difference between the volume of foliage present for both the total avifauna and the 5 selected bird species. Douglas-fir and Engelmann spruce were strongly
Table 1
Tree Species Density, Importance Value, and Foliage Volume

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Tree density (#/ha)</th>
<th>Importance value*</th>
<th>Foliage volume (m³/ha)</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ponderosa pine</td>
<td>112.7</td>
<td>67.8</td>
<td>40910.4</td>
<td>35.9</td>
</tr>
<tr>
<td>Southwestern white pine</td>
<td>109.6</td>
<td>46.7</td>
<td>40253.3</td>
<td>35.3</td>
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<tr>
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<td>3.1</td>
<td>1.5</td>
<td>181.7</td>
<td>0.2</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>194.1</td>
<td>92.3</td>
<td>20000.5</td>
<td>17.6</td>
</tr>
<tr>
<td>White fir</td>
<td>51.7</td>
<td>24.5</td>
<td>4305.5</td>
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<tr>
<td>Blue spruce</td>
<td>12.5</td>
<td>5.2</td>
<td>552.6</td>
<td>0.5</td>
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<tr>
<td>Englemann spruce</td>
<td>31.3</td>
<td>13.0</td>
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<td>2.0</td>
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<td>Quaking aspen</td>
<td>50.1</td>
<td>20.3</td>
<td>5565.9</td>
<td>5.0</td>
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<tr>
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<td>61.1</td>
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<td>—</td>
</tr>
<tr>
<td>Total</td>
<td>626.2</td>
<td>300.0</td>
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<table>
<thead>
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<th>Tree species</th>
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<th>Importance value*</th>
<th>Foliage volume (m³/ha)</th>
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</thead>
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<tr>
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<td>8.8</td>
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<td>12.6</td>
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<td>Douglas-fir</td>
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<td>30.5</td>
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<tr>
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<tr>
<td>Snag (dead tree)</td>
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<tr>
<td>Total</td>
<td>167.7</td>
<td>300.0</td>
<td>15269.9</td>
<td>100.2</td>
</tr>
</tbody>
</table>

*Importance value is the sum of relative density, relative dominance, and relative frequency.

preferred, whereas ponderosa pine, southwestern white pine, and aspen were seldom used.

In both habitats the 5 avian species preferred spruces and firs and used the pines, aspen, and snags less than expected (Figs. 2–6). There were several exceptions to these generalizations. For example, Yellow-bellied Sapsuckers (Fig. 2) frequently foraged on snags in both habitats. No significant difference between use and availability was found for Douglas-fir or white fir in the unlogged site or for blue spruce and Englemann spruce in the logged site.

It may be argued that since Yellow-bellied Sapsuckers confine most of their activities to tree trunks, a comparison of sapsucker use to tree species density
TREE SPECIES PREFERENCES
ALL BIRDS
UNLOGGED AREA

AVIAN USE
FOLIAGE VOLUME
RELATIVE DENSITY
N = 4648

TREE SPECIES

TREE SPECIES PREFERENCES
ALL BIRDS
LOGGED AREA

AVIAN USE
FOLIAGE VOLUME
RELATIVE DENSITY
N = 4964

Fig. 1. Tree species preferences of all birds in the unlogged and logged areas. Plain bar is % of avian use. Crosshatched bar is % of foliage volume for the given tree species. Hatched bar is relative density of snags. Tree species were abbreviated as follows: PP—ponderosa pine; SWWP—southwestern white pine; AF—alpine fir; DF—Douglas-fir; WF—white fir; BS—blue spruce; ES—Englemann spruce; and ASP—quaking aspen.
Fig. 2. Tree species preferences of the Yellow-bellied Sapsucker in the unlogged and logged areas.
Fig. 3. Tree species preferences of the Mountain Chickadee in the unlogged and logged areas.
Fig. 4. Tree species preferences of the Ruby-crowned Kinglet in the unlogged and logged areas.
Fig. 5. Tree species preferences of the Yellow-rumped Warbler in the unlogged and logged areas.
Fig. 6. Tree species preferences of the Gray-headed Junco in the unlogged and logged areas.
might be more appropriate than a comparison to foliage volume data since presumably this species would be less dependent on the volume and type of foliage present than would be, for example, a foliage-gleaning species. However, the density of individual tree species is positively correlated with foliage volume per tree species \( r = +.69 \) unlogged area, \( r = +.41 \) logged site).

Results for the sapsucker were graphed in a consistent manner with the representation of the other 4 species and with the total avifauna.

For the Ruby-crowned Kinglet there was no significant difference between frequency of use and proportion of foliage volume present in alpine fir and blue spruce in the lumbered section (Fig. 4). The kinglet was rarely observed on snags.

The Yellow-rumped Warbler in the unharvested area (Fig. 5) visited ponderosa pine and southwestern white pine more frequently than did the other 4 avian species examined in detail. In the modified site, aspen was also frequently used, but far less than expected on the basis of tree availability.

Gray-headed Juncos in the unaltered habitat used alpine fir and aspen in proportion to their availability (Fig. 6). Tree use in the harvested area could not be associated with tree availability.

The Ruby-crowned Kinglet had a higher niche breadth value (Table 2) in the unlogged area than in the modified site. In contrast, the Mountain Chickadee and Gray-headed Junco showed higher values in the logged area. Niche breadths for both the Yellow-bellied Sapsucker and Yellow-rumped Warbler were similar in the modified and virgin forests. For the unaltered habitat, the Yellow-bellied Sapsucker \( (B = 2.00) \) had the highest niche breadth value followed by the Yellow-rumped Warbler \( (B = 1.91) \). These 2 species also had the highest values for the modified area, \( B = 1.93 \) and \( B = 1.96 \), respectively.

Although the Mountain Chickadee and Ruby-crowned Kinglet displayed strong preferences for the same tree species there were differences in terms of proportion of use. In the unmodified site the Mountain Chickadee used

<table>
<thead>
<tr>
<th>Bird species</th>
<th>Unlogged</th>
<th>Logged</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellow-bellied Sapsucker</td>
<td>2.00</td>
<td>1.93</td>
</tr>
<tr>
<td>Mountain Chickadee</td>
<td>1.74</td>
<td>1.90</td>
</tr>
<tr>
<td>Ruby-crowned Kinglet</td>
<td>1.71</td>
<td>1.46</td>
</tr>
<tr>
<td>Yellow-rumped Warbler</td>
<td>1.91</td>
<td>1.96</td>
</tr>
<tr>
<td>Gray-headed Junco</td>
<td>1.72</td>
<td>1.90</td>
</tr>
</tbody>
</table>

\* Niche breadth = \(-\sum p_i \ln p_i\)
Table 3

<table>
<thead>
<tr>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td>Yellow-bellied Sapsucker</td>
<td>15.8</td>
<td>10.6</td>
<td>20.5</td>
<td>10.2</td>
</tr>
<tr>
<td>Mountain Chickadee</td>
<td>11.8</td>
<td>44.7</td>
<td>30.8</td>
<td>58.9</td>
</tr>
<tr>
<td>Ruby-crowned Kinglet</td>
<td>42.1</td>
<td>71.0</td>
<td>23.1</td>
<td>74.4</td>
</tr>
<tr>
<td>Yellow-rumped Warbler</td>
<td>100.0</td>
<td>131.6</td>
<td>76.9</td>
<td>89.8</td>
</tr>
<tr>
<td>Gray-headed Junco</td>
<td>76.3</td>
<td>31.6</td>
<td>74.4</td>
<td>51.3</td>
</tr>
<tr>
<td>Total avifauna</td>
<td>544.0</td>
<td>632.9</td>
<td>758.0</td>
<td>865.9</td>
</tr>
</tbody>
</table>

Douglas-fir 40.9% and Engelmann spruce 13.6% of the time. However, the Ruby-crowned Kinglet frequented Engelmann spruce 45.8% and Douglas-fir only 22.7% of the time. A slightly different situation occurred in the logged site where the Mountain Chickadee was less specialized in its tree species use, selecting Douglas-fir and Engelmann spruce a total of 48.1%, whereas the Ruby-crowned Kinglet relied heavily on these 2 tree species (82.6% of its total foraging observations).

Avian densities.—The unmodified habitat supported a considerably larger avian community (Table 3) than did the logged site during the breeding season of each year. The Mountain Chickadee, Ruby-crowned Kinglet, and Yellow-rumped Warbler were more numerous in the virgin forest than in the lumbered site. Gray-headed Juncos were much commoner and Yellow-bellied Sapsuckers were slightly more numerous in the harvested site than in the unlogged area.

Discussion

There are various possible explanations for avian selection of certain tree species while not using others. Factors affecting tree selection include food abundance, availability, and quality. Foliage may be important for birds in that it protects them from predators and inclement weather conditions and shelters the nest sites of numerous species.

In examining foraging behavior of English titmice (*Parus* spp.) Hartley (1953) found that although every tree species was used, some were far more intensively used. Tree species selection, in addition to height distribution and the tendency to search for food in different parts of the trees, permitted 5 species of titmice to occupy the same habitat. During periods of superabundant food supply, the ecological distinctiveness in feeding behavior disappeared among the 5 congeneres, indicating the importance of competition for
food in determining foraging behavior (Hartley 1953). Studies by Palmgren (1930), Kluijver (1951), Gibb (1954), and Jackson (1970) also noted avian selection of certain tree species. However, Brewer (1963) stated that the Black-capped \textit{(Parus atricapillus)} and Carolina chickadees (\textit{P. carolinensis}) appeared to use the vegetation in relation to its abundance in the habitat in Illinois. Perhaps no habitat partitioning was evident in these species because they are primarily allopatric; moreover, Brewer suggests that competitive interactions may be a factor in producing this allopatry. Habitat partitioning achieved, in part, by tree species selection in Willow Creek was probably of more importance to some species than to others. No 2 species had exactly the same tree species preferences. Some potential competitors such as the Mountain Chickadee and Ruby-crowned Kinglet spent different proportions of their time in the same tree species. In the absence of data on abundance and locations of the food supply, it is not possible to state with certainty that competition for food was responsible for this habitat partitioning. In addition to tree species selection a variety of other possible mechanisms such as within-tree location preferences (Franzreb 1976), tree height selection, and foraging behavior (Franzreb 1975) were involved in habitat segregation.

During the nesting season the majority of birds in Willow Creek are insectivorous. The availability and type of food source may influence which trees birds prefer. Southwood (1961) found that the number of insect species associated with given tree species varied in Britain. Among genera of trees in his study (and which occurred in Willow Creek), poplars \textit{(Populus)}, pines \textit{(Pinus)}, spruces \textit{(Picea)}, and fir \textit{(Abies)} had 97, 91, 137, and 15 insect species respectively. Overall insect abundances were not derived, hence, it was not known which tree species harbored the greatest densities of insects. Birds may select trees with only a few insect species if such prey items occur in sufficient numbers to make exploitation efficient. Insect abundance and number of species may also have varied among the tree species in Willow Creek.

The amount of vegetation present may influence insect numbers as evidenced by the number of foraging observations in heavy foliage. Successful foraging, however, is not solely dependent on the number of prey items per tree, but is more closely related to the density of insects (number per unit foliage volume). Search time required between successful captures, flying time between foraging sites, handling time per prey item, and the individual’s degree of prey specificity may determine a bird’s competency in exploiting a given resource. Those individuals selecting the portions of the habitat in which it is possible to achieve the highest degree of foraging success will have an advantage.
In the unlogged study area in Willow Creek, ponderosa pine and southwestern white pine, the tree species which contained the greatest amount of foliage volume were used far less than other tree species containing smaller amounts of foliage such as Douglas-fir and Engelmann spruce. Also, for the timber harvested area quaking aspen comprised 53% of the total available foliage and accounted for less than 15% of the total avian observations. However, foliage volume calculations were based on formulae which did not consider that pine and aspen leaves or needles are much less dense than those of spruces and firs. Therefore, the foliage per unit volume probably was much higher for the latter tree species than for the former. Hence, the disparity between avian use and calculated available foliage for some tree species may not be as great as shown.

Possibly the majority of birds infrequently visited pines and aspen because it was not energetically economical to use them. Perhaps search time was so prolonged that in all but the choicest sections of these trees, exploitation was impractical. Increased exposure to predators and inclement weather resulting from the openness of the vegetation may also have discouraged birds from using these species.

Snags harbor a variety of insects, many lying between the crevices on the bark or under the bark’s surface, thus necessitating special morphological adaptations such as in the tongue or in the length and shape of the bill, to provide accessibility to prey. The many typically foliage-gleaning species in Willow Creek lack the necessary adaptations to extensively use snags but are adapted for exploiting live trees. Snags also harbor a different insect fauna than found in live trees (Anderson 1960). Difficulty in securing food as well as the type of insect prey available in snags, may have prevented or discouraged many birds, particularly foliage gleaners, from extensively using them.

Leaf morphology and size may influence the degree of avian use of a given tree species. The large leaf size of quaking aspen make it difficult for the majority of these birds, particularly the smaller passerines, to perch on an aspen branch or twig and reach the middle and outer portions of the leaves which may harbor insects. Hovering forms such as the Ruby-crowned Kinglet may encounter difficulty since aspen leaf movement occurs with even slight breezes. Further, aspens may not support similar insect densities and species found in coniferous trees.

Niche breadth values derived from tree species use data for individual bird species indicated differences existed between the unlogged and modified sites. In this context, I used the spatial model for the niche proposed by Hutchinson (1958) and expanded by Slobodkin (1962), Levins (1968), and MacArthur (1968). Avian niche breadth was considered as the degree of
diversity in tree species selection. It is the inverse of the degree of ecological specialization of a particular species within a given habitat (Levins 1968). Niche breadth does not indicate anything about tree species availability and is only suggestive of the evenness of tree species use for a particular bird species.

It is possible that very stereotyped species in the logged site which did not occur in sufficient numbers to be studied, were among the most affected by habitat modification. For example, logging in effect eliminated the Brown Creeper (*Certhia familiaris*), thus making it impossible to compare its foraging behavior in the 2 study areas. Perhaps those species present in sufficient numbers in both habitats to afford an adequate sample size, were the most plastic species, yet 1 of the 5 appeared to be fairly stereotyped in its foraging behavior (Ruby-crowned Kinglet). Stereotyped species should show a reduction in density and/or niche breadth in the modified site since they, presumably, restricted their activities to only the most useful tree species. This was true for the Ruby-crowned Kinglet. Such species may have enlarged territories in order to be assured of access to the minimum essential number of preferred trees. Thus, the number which the logged habitat could support would be reduced.

A more generalized species which maintained its density in the logged site map show a concomitant increase in niche breadth since it was possible to switch to normally infrequently visited tree species. A species might undergo a reduction in density in the modified site if either its niche breadth value was approximately the same in the 2 study sites (i.e., it could not become more generalized) or if the niche breadth value increased. The former situation was found for the Yellow-rumped Warbler and the latter for the Mountain Chickadee. Apparently the logged habitat was incapable of supporting as many Mountain Chickadees as the unmodified site. Perhaps this resulted from an insufficient amount of foliage volume of the favored tree species to fulfill all their requirements.

If a species, such as the Gray-headed Junco, achieves a higher density in the altered site than in the virgin forest, it may be fairly plastic and hence, exhibit an increase in niche breadth. Gray-headed Juncos were more numerous and had a higher niche breadth value in the logged than unlogged site. This junco, primarily a ground foraging species, is not as specific in its tree species selection as are foliage-gleaners. The Juncos also used slash (logging debris) which was abundant following lumbering. Slash provided an additional substrate which probably contributed to their higher density there.

Some species may have concentrated on the preferred tree species in order to acquire essential resources such as food, or perhaps it was a useful
strategy to further segregate the habitat among species in the logged site which may have been a more limited environment. Others may have become more generalized in order to take advantage of a larger portion of the habitat. Apparently avian species adjusted in various ways to the reduction in foliage volume and the reapportionment of the available foliage to different tree species in the harvested environment.

Future management decisions pertaining to timber harvesting should consider the heavy use of spruces and firs by birds. A decision to remove a substantial proportion of pines and aspen even though they are not frequently used by the avifauna, would adversely affect a number of species which rely upon these trees for nesting such as the Yellow-bellied Sapsucker and Warbling Vireo (*Vireo gilvus*) which nest in aspen, and for foraging such as the Grace’s Warbler (*Dendroica graciae*) which forages in pines. I recommend that areas not be logged as heavily as Willow Creek which underwent a moderately-heavy overstory removal (removal of most of the trees forming the forest canopy). The majority of snags should not be harvested as they serve several significant functions such as providing nest sites for numerous cavity-nesting species.

**SUMMARY**

Variation in avian selection of tree species in a community which had undergone an overstory removal form of timber harvesting was compared to a virgin, mixed-coniferous forest, in the White Mountains, Arizona, during the summers of 1973 and 1974. Tree species preferences for all birds observed indicated Douglas-fir, white fir, and Engelmann spruce were the most frequently visited species in both habitats and were used in both the unmodified and logged areas in excess of the proportion of foliage volume they contained in the entire habitat. Ponderosa pine and southwestern white pine were frequent less than expected on the basis of availability. Although aspen constituted over 50% of the available foliage in the harvested habitat, birds did not appear to compensate for the reduction in density of firs and spruces by increasing their use of it. Whereas some species in the modified environment, such as the Mountain Chickadee, became more generalized and therefore less selective as to tree species, the Ruby-crowned Kinglet apparently became more restricted, and hence, more specialized in tree species preferences. Use of quaking aspen, the only species not removed during harvesting, and snags (dead trees) was higher in the modified than in the unaltered habitat.

**ACKNOWLEDGMENTS**

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LITERATURE CITED


BUREAU OF LAND MANAGEMENT, 1695 SPRUCE STREET, RIVERSIDE, CA 92507. ACCEPTED 15 JULY 1976.
DOUBLE-BROODEDNESS IN PURPLE MARTINS IN TEXAS

CHARLES R. BROWN

Most ornithologists consider Purple Martins (Progne subis) to be single-brooded throughout their range, although this is a somewhat controversial topic. Allen and Nice (1952), Lee (1968), Layton (1969), and Lowery (1975) stated that martins are single-brooded with little or no evidence of double-broodedness. Yet Forbush (1929), Baerg (1931), and Sprunt (in Bent 1942) believed the birds to be double-brooded; Audubon (1840) mentioned third broods in Louisiana. Peterson (1941) and Harrison (1975) indicated that martins occasionally raise second broods in the southern United States. Johnston and Hardy (1962) recognized martins as usually single-brooded but reported second broods in southern Illinois.

Allen and Nice (1952) questioned all second broods, providing testimonials from southern martin fanciers to the effect that there is insufficient time during the martin’s breeding season for double broods. Skepticism might arise from a lack of details regarding reports of double-broodedness. Despite the several references to second broods, the only detailed report in the literature is my (1973) account of a second brood in 1970 in north central Texas.

In 1976–1977 I observed 6 additional second broods by Purple Martins in north central Texas. This paper will explain these occurrences, analyze environmental conditions and stimuli, and offer an hypothesis regarding double-broodedness in Purple Martins.

DESCRIPTION OF THE MARTIN COLONY

The martin colony was located in my residential backyard within the city of Sherman, Grayson County, north central Texas. In 1976–1977 the colony contained 110 and 72 apartments respectively and consisted of 7 and 4 martin houses of various sizes and designs. Fourteen other active martin colonies were located within a 1.6 km radius from my colony. Prior to 1976 martins had nested at this location for 8 years.

In 1976, 35 pairs of martins attempted to nest in my colony. Of those, 18 (51.4%) appeared to be adult pairs and 17 (48.6%) appeared to be subadult (i.e., 1st year) pairs. Sixteen (45.7%) pairs raised 1 brood and fledged young on the first attempt. Six (17.1%) pairs raised 1 brood and fledged young on the second attempt, having failed for various reasons on the first attempt. Nine (25.7%) pairs failed to fledge young on either attempt. Four (11.4%) pairs fledged second broods. In 1977, 27 pairs of martins nested in the colony, but I did not collect detailed breeding data for that year.
The 1976 figures were compiled after intensive surveillance of the martin colony throughout the breeding season. I closely watched the colony for several hours each day from the arrival of the first martins in February until the last brood departed in August. I made nest checks daily. An assistant and I banded 638 martins in the Sherman area in 1974–75. Several of these banded martins were present at my colony in 1976.

**OBSERVATIONS**

I spent 1000 (±5%) h watching the martin colony during the breeding season of 1976. My intense surveillance of the colony was significant since 3 of the 4 pairs involved in second broods were unmarked. I spent many hours watching these birds and am fully convinced of the validity of the results. Individual recognition of unmarked birds is discussed further below.

**Pair 1:** An all-purple adult male and an adult female arrived at the colony on 20 February 1976. In contrast to many martins that claim several rooms in the early part of the season, this pair claimed only 1 room throughout the breeding season. Four young of their first brood left the nest on 29 May. After the young fledged, the adults led them back to the nest compartment to roost nightly until 5 June.

On 5 June I began noticing Pair 1 perching by their nest and entering the nest compartment. I assumed that the young had become independent and that the adults were displaying post-breeding nest defense. Post-breeding nest defense is common among martins. No juveniles returned to the nest on 5 June nor at any time afterward. Pair 1 remained at the colony for long periods on 5–15 June but never brought nesting materials to the nest during that time. On 16 June one egg was laid in the old nest, followed by another on 17 June. The female began incubation on 17 June after laying the second egg. The male was quite attentive to the female while she incubated, and although male Purple Martins do not incubate, he frequently guarded the nest when she was away. He also brought green leaves to the nest while the female incubated.

The eggs hatched on 2 July. Both parents fed the young until they were about 3 weeks old. At that time the male gradually stopped feeding. He had ceased feeding completely by the time the young were ready to leave. However, he often appeared and perched by the nest, and he and the female were never hostile toward each other. When the young were about 2 weeks old, the female ceased roosting in the nest and disappeared from the colony each evening at dusk. Each morning she reappeared quite early. The male had stopped roosting at the colony during the incubation period. One young left the nest on 28 July, and the other left on 29 July. No juveniles returned to roost in the nest after 29 July, and the parents rarely appeared.
The unmarked male had no outstanding trait, but from watching his behavior very closely for many hours, I am convinced that the same bird was engaged in both broods. The unmarked female was easy to recognize. She was very white on the lower breast and belly, appearing much lighter than other females that arrived in February. She also had a peculiar habit of running along the entire length of the porch of the martin house before flying. She exhibited this peculiarity during both nestings.

**Pair 2:** Adult male arrived at colony on 24 February 1976 and began claiming a tier of 4 nest compartments. An adult female arrived on 2 March and established a pair bond with the male. Four young of a first brood fledged from Pair 2’s nest on 31 May and 1 June. Soon after the young left, 1 noticed another adult male claiming this tier of 4 rooms. When Pair 2 attempted to lead their young back to the martin house to roost on 1 June, this new male attacked the juveniles and their male parent, but allowed the female to land on the house and enter her nest. He would not allow the juveniles or male parent to roost in the nest or anywhere else on the tier. The female attempted to lead 1 or 2 of her young back nightly until 8 June, but the new male never allowed the juveniles to roost. He tolerated the female though and frequently courted and sang to her.

On 8 June the female began perching by the nest for long periods, and the new male appeared to establish a pair bond with her. This “revised” Pair 2 spent much time sitting on the martin house on 8–12 June but never brought nesting materials to the house. On 13 June an egg was laid in a room adjacent to the former nest compartment. A small nest was in this new compartment, having been built by this same female earlier in the season when she was building in all rooms on the tier. She laid 1 egg daily until 18 June when she laid her 6th and final egg and began incubation. Her new mate was delinquent in guarding the nest during the incubation period, rarely appeared to guard in the afternoon, and rarely gathered green leaves.

The eggs hatched on 3 July. The female did considerably more feeding of the young than did the male. Daily 2-hour watches of this pair revealed that the female was responsible for 70–83% of the total feeding trips. However, as the young became older the male appeared to develop stronger parental instincts. When the young came out on the porch of the house 2 days prior to leaving, the male guarded them virtually constantly while the female fed them. Three young left on 29 July and 2 left on 30 July. One nestling had disappeared from the nest a week earlier. The female roosted in a room of the tier each night throughout the second nesting, but the male had ceased roosting at the colony during the incubation period. The adults did not lead the juveniles back to the nest to roost after 31 July.

Many times as I watched this new male of Pair 2, he sang to a female that
was feeding young on the tier below him. He often flew down to her and entered her nest. I saw him feed this female’s young twice after finding his young unresponsive, and he appeared to be a partial polygynist (See Brown 1975).

The original male of Pair 2 was easy to separate from the new male that took over the nest after the first young left. The original male’s purple under tail coverts were extensively edged with white. No other males in the colony had such markings. From watching the unmarked female closely during both broods, I am confident that she was the same individual involved in both. During both broods, she was unusually aggressive toward a pair of House Sparrows (Passer domesticus) that nested in a room on a lower tier. She attacked the sparrows whenever she flew from the house. Also, while feeding her second brood, she often first entered her nest of the first brood, then “remembered” her second brood in the adjacent hole and moved to it.

Pair 3: An adult male arrived on 18 March 1976 and established himself in the attic hole of a small wooden martin house. He attracted an adult female on 21 March. Three young of a first brood fledged from Pair 3’s nest on 6 June. They brought their young back to the house to roost nightly on 6–14 June. On 15 June I noticed Pair 3 perching by and entering their nest. I often saw them near the nest on 15–19 June, but I never saw them bring nesting materials to the nest during that time. On 16 June I saw several males chasing the female of Pair 3 in a “rape” flight while her mate tried to fight them off. I had never before seen a rape that late in the season. Rape flights by martins are frequent in Sherman, Texas, in March, April, and May while the birds are courting, but are very rare anytime in June.

On 20 June 1 egg was laid in the nest, followed by 1 a day until 24 June when the 5th and final egg was laid and the female began incubation. The male was very attentive to his incubating mate and often guarded the nest when she was away, but he rarely brought green leaves. The eggs hatched on 9 July. Both parents fed the young throughout the nestling period. Neither adult fed at a greater rate than the other. Neither parent roosted at the colony after the young were about 2 weeks old. Three young left the nest on 6 August, and 2 left on 7 August. The parents did not lead them back to the nest to roost after leaving.

This male wore U.S. Fish and Wildlife Service band no. 772-05364. I confirmed this number with a 30X telescope and by capture during both nestings. He had been banded as a nestling at a nearby colony in Sherman in 1974 and nested at my colony in 1975. The female was quite easy to distinguish from all other martins in the colony since the second, third, and fourth primaries of her left wing were missing. The feathers were gone when she
arrived in March, and no noticeable replacement occurred during the breeding season. No other martin in the colony had such a noticeable “gap” in its wing.

Pair 4: An adult female arrived at the colony on 20 February 1976 and began claiming a tier of 4 nesting compartments. An adult male, who was paired to another female on an upper tier, showed interest in the female of Pair 4 and claimed her until 6 March when another adult male arrived and established a pair bond with her. Four young of their first brood fledged on 11 June. After the young fledged, Pair 4 led them back to the nest to roost nightly until 20 June when I noticed the parents perching by the nest for great periods. The juveniles did not return to the nest after 19 June.

Pair 4 spent much time sitting by, and in, the nest on 20–25 June, but never brought nesting materials to the nest during that period. One egg was laid in the nest on 26 June, followed by 1 a day until 29 June when the female laid her 4th and final egg and began incubation. The male was quite attentive to her while she incubated and often guarded the nest when she was away. Virtually every morning until the eggs hatched, this male spent several hours constantly gathering green leaves and bringing them to the nest.

The eggs hatched on 14 July. Both parents fed the young at about equal rates until the young were about 3 weeks old. On 5–6 August the female ceased feeding completely. During the last week before the young left, only the male fed them, and the female only occasionally appeared and sat by the nest. She and the male were never hostile toward each other. All 4 young fledged from the nest on 11 August. The male did not lead them back to the nest to roost after leaving. Both parents ceased roosting at the colony after the young were about 2 weeks old.

The unmarked male had a throat mottled with purple and brown. He was the only all-purple adult male martin I saw that was not uniform purple on the throat. The unmarked female was an old appearing bird, and her breast and belly were largely fuscescent instead of dark gray. Her brownish breast contrasted sharply with her purple back. She also had an extremely vertical posture whenever she sat on the martin house. I am convinced that the same individuals were involved in both broods.

Colonial Activity 13 June–11 August: From 13 June 1976 when the earliest egg of a second brood was laid until 11 August when the young of the last second brood departed, 21 martin pairs in the colony were engaged in various nesting stages of first broods. The activity of these pairs is summarized in Table 1.

Large numbers of martins visited the colony throughout 13 June–11 August. I often saw 70 or more martins perched on martin houses and wires around the colony while the second broods were in progress. Most of these were birds
that had completed breeding, but many were juveniles. Martins were present during most of the day, with largest numbers appearing in the morning. I had never seen such large numbers around the colony in mid- and late July and early August. The many martins around the colony in July reminded me greatly of a thriving colony in June. My studies indicate that many martins becoming post-breeding vagrants and visit colonies in their local area after finishing breeding. They show no definite breeding tendencies but sit on the wires and preen and alight on the martin houses. During Pair 4's last week, very few martins appeared at the colony in the mid-afternoon hours, and Pair 4 reduced the frequency of feeding at that time.

DISCUSSION

I became fully convinced in 1976, through observations of 1 marked and 3 unmarked pairs, that Purple Martins occasionally raise second broods. However, the color banded pairs in 1977 provide unequivocal evidence that Purple Martins are sometimes double-brooded. Since most field work was performed in 1976, the following discussion is based only on the 1976 double-brooded pairs and the breeding season of 1976.

All 4 double-brooded pairs displayed normal breeding behavior while raising second broods. I noted no appreciable behavioral differences among the 4 pairs. They differed from first broods in only 2 aspects, both of which are probably insignificant. None of the pairs built a nest for their second brood, but all already had nests. Three pairs used the original nest hole for their second brood, while 1 used an adjacent compartment. None of the pairs led the young of their second brood back to the nest to roost for a long period after fledging. However, this was probably because the adults themselves were no longer roosting in the nest. I saw many martins of the neighborhood
use a grove of eastern cottonwoods (*Populus deltoides*) for roosting each evening in July and early August.

The male of Pair 1 and the female of Pair 4 ceased feeding the young of their second brood before the young fledged. This loss of parental care may be attributed to the lateness of the season, particularly in Pair 4’s case. During the last week when the female of Pair 4 had stopped feeding, I noticed many male martins around the colony but few females (often 25–35♂♂:1♀), suggesting that females may move to the pre-migratory roosts earlier than males.

Two of the double-brooded males often brought green leaves to the nest during incubation. These double-brooded males gathered more leaves than many single-brooded males, particularly single-brooded subadults.

All double-brooded martins observed were adults. Since adults arrive on the breeding grounds before subadults, it is likely that all second broods in martins are raised by adults. There is no time for later-arriving subadults to rear second broods.

It is probable that all 4 double-brooded pairs successfully fledged their first brood to independency. If the young of a first brood succumbed shortly after leaving the nest, the parents’ subsequent second brood might be a re-nest. This is unlikely in my cases though. All 4 pairs led their first brood back to the nest to roost for a week or longer. It is likely that young martins become independent 7–10 days after leaving the nest but I have not determined the true time required for young to become independent.

Regarding Lowery’s statement (*in* Allen and Nice 1952) that late nesters may occupy the nest sites after the original martins fledge young and can be confused as second broods, I have found that even after fledging young, many martins maintain close ties with the nest. Most pairs bring their young back to the nest to roost nightly. Returning with the young at night serves to discourage other martins from moving into the nest. Of my double-brooded pairs, only the male of Pair 2 was displaced by an outsider who appropriated the nest after the young fledged. I might also add that at my colony in 1976 there were large numbers of vagrant martins that would have likely moved in had the double-brooded martins not discouraged them by returning each evening with their young. A further deterrent to outsiders moving in is well-pronounced post-breeding nest defense in martins. Post-breeding nest defense has been noted often in my studies and by Finlay (1971).

I began sponsoring Purple Martin propagation efforts in the city of Sherman, Texas, in 1973–76 as an aid to my martin studies. Few martin houses were present in the city in 1968 when I began studying martins and in 1970 when I noted an unsuccessful second brood attempt. By 1976 the number of
martin houses in the city had increased 550%. Populations of Purple Martins increased similarly or more so.

Most martins in Sherman normally finish nesting activities in mid- to late June. Until 1976 I had never recorded martins breeding at my colony after 10–15 July. A second brood in 1970 failed on 14 July. Few martins were present around the colony then (Brown 1973). Numbers of post-breeding vagrant martins that visit the colony also greatly decrease after 10–15 July. Until 1976 I had rarely seen over 30 martins at the colony in late July and August. I made a check of other colonies in Sherman in late July and found few martins around any of them except mine and one small and newly-established colony. An adult pair of martins at this small colony was feeding young in early August. I suspect that this was also a second brood, but I have no proof.

I was impressed by the many martins that raised first broods at my colony in July (and 1 pair in August). More birds in 1976 led to many that were unable to find breeding places until late May and early June. Consequently these birds were still nesting in July. Purple Martin populations apparently exploded in the Sherman area in 1976, resulting in many pairs nesting later than usual. The presence of many martins late in the season undoubtedly provided a stimulus for the rearing of second broods by pairs that fledged young earlier. This is consistent with the second brood attempt in 1970 (Brown 1973).

Johnston and Hardy (1962) believed that very mild and unseasonable weather in southern Illinois provided stimulus for second broods in that area. But in Sherman, Texas, in 1976 weather conditions were normal, and the first arrivals did not begin nesting any earlier than in past years. Presence of other martins late in the season apparently outranks weather conditions as second brood stimulus for martins in north central Texas. Thus, I suggest that second broods by Purple Martins may occur in the southern U.S. whenever large numbers of martins are present at the colonies later than usual. Such numbers may be due to either local population increases or nesting disasters in the early part of the season.

Since most martins leave the Sherman area in mid- to late August, presumably on fall migration, juveniles of second broods have less time before migrating to increase fat reserves and become proficient at catching insects. This could result in greater mortality among juveniles of second broods which would limit any inherited double-broodedness in a local Purple Martin population.

SUMMARY

Four adult pairs of Purple Martins in a colony of 35 pairs in Sherman, Texas, successfully fledged second broods in the breeding season of 1976. Two additional pairs raised
second broods in 1977. Breeding behavior of these second nestings was studied and was found not to differ significantly from breeding behavior of first nestings.

Purple Martin propagation efforts in Sherman, Texas, in 1973–76 resulted in great numbers of martins in the local area in 1976. Many martins were unable to find breeding places in the early part of the season and raised their first broods much later in the season than usual. Such late nesting apparently served as a stimulus to the raising of second broods by pairs that fledged young earlier. Purple Martins may raise second broods in the southern part of their range whenever large numbers of martins remain at the colonies later than usual.

LITERATURE CITED


BOX 1309, AUSTIN COLLEGE, SHERMAN, TX 75090. ACCEPTED 3 DEC. 1976.
FOOD OF NESTLING PURPLE MARTINS

Helene Walsh

Post-fledging survival of young passerine birds appears to be strongly influenced by the quantity of food received while in the nest (Perrins 1965). A number of studies have been done to determine how much nestlings are fed but few (e.g., Royama 1966) have involved the greater part of the nestling period.

Finlay (1971) used mechanically recorded visits to the nest cavity as an index of feeding activity in Purple Martins (Progne subis). He assumed that food was brought to the nestlings on each visit. His results showed an increase in visits to the nest cavity with increased brood size, but the increase was not proportional to the number of nestlings involved. Finlay's study raises a number of questions concerning amount of food fed to individual nestlings in broods of various sizes: (1) are parent birds able to maintain constant energy intake by individual nestlings when brood sizes are larger by increasing the proportion of feeding visits to the nest or, (2) can they compensate for a larger brood by bringing either a greater biomass of food per feeding visit or, (3) does the decreased surface-area-to-volume relationship in larger broods enable individuals to maintain themselves sufficiently on a lower biomass of food? I tried to answer these questions in Finlay's study area on the shore of Aostin Lake (53° 40' N, 112° 50' W) in Elk Island National Park, Alberta, where martins were nesting colonially in artificial nest boxes during the summers of 1970 and 1971.

MATERIALS AND METHODS

To answer the above questions I obtained qualitative and quantitative measurements of food brought to nestling Purple Martins and analyzed these data with respect to brood size, age of nestlings, time of day, and season. Unless otherwise stated the test for significance used was Wilcoxon's signed rank test (Steel and Torrie 1960) and the accepted level of significance was P < .05.

Nest boxes.—Purple Martins had inhabited the 4 wooden houses used during the study for several years. I built an observation blind behind each house and had easy access by moving a black cloth covering the back of each 18 cm² nesting compartment. A periscope fastened over an opening in this cloth let me view activities without alarming the birds.

Martin population.—Because the colony size was so small all nesting pairs were studied in both years. In 1970 2 of the 4 pairs started laying about 1 week before the others. Nestlings that hatched and survived were rearranged in these 2 nests to give broods of 3 and 2, to match those of the second 2 pairs of martins. In all nests some nestlings died, probably a result of asynchronous hatching—the younger birds apparently could not compete successfully for food. All the nestlings except for 2 in the older brood of 3

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young died on the same day at the ages of 23 and 14 days, probably as a result of 3 consecutive cold rainy days.

In 1971 two broods were studied; 1 brood of 2 nestlings that hatched 8 July, and in which 1 nestling died on day 19, and 1 brood of 4 nestlings, which hatched 14 July, and in which 2 nestlings died on day 12. The above deaths were accidentally caused by a food digestion study and resulted in brood sizes 2 and 1.

**Food and food value.**—The diet of nestlings was determined by collecting food given them from days 2 to 23 post-hatching, using the method of placing a piece of pipe cleaner around the neck of the nestling just tightly enough to prevent swallowing (Orians 1966). After a feeding visit the nestling was immediately removed from the nest and the food forced up to the beak by massaging the throat. Food gathered by this technique was placed in a vial for subsequent weighing and identification. The volume of food collected from each nestling was replaced by an approximately equal volume of food that I caught.

Insects were identified to family with the aid of keys (Jaques 1947, 1951). A determination of the calorific value of the most common insects in the samples representing different families was done (Spice 1972) but results were inconclusive.

**Food collection periods.**—Collection of food samples at any one nest did not exceed 2 consecutive hours, with at least 4 h intervals between collections. Collection of food terminated when nestlings were about 21 days old; at this age food began slipping past the pipe cleaner, presumably a result of strengthened esophageal musculature. Nestlings were weighed each day at about 18:00.

The birds’ activities at the nest were monitored by me over time periods varying from 1 to 3 h. Movements by adult martins in and out of the nest cavity were registered by a mechanically activated event recorder.

**Weather.**—Data on meteorological conditions were collected at the colony site in both years. Readings of light intensity, wind speed, temperature, and relative humidity were made immediately before and after the observation and collection periods. General weather data were obtained from the Edmonton International Airport, about 48 km from the study area.

**RESULTS AND DISCUSSION**

Of 956 food samples collected from the nestling martins, 246 were collected between 8 and 29 July 1970 from 4 broods, and 710 samples were collected between 15 July and 11 August 1971 from 2 broods.

**DIET OF NESTLINGS**

**Influence of time of year on diet.**—Families of insects contributing more than 1% of the total weight of food collected in either year are listed in Table 1. Relative use of insect families differed between years; for the Nymphalidae this difference was significant ($\chi^2, P < 0.05$) and appeared to reflect both the 7 days’ difference in initiation of the nestling season, and the premature deaths of the nestlings on 29 July 1970. In 1971 the study terminated on 11 August, 13 days later than in 1970. The mourning cloak butterfly (*Nymphalis antiopa*) was the species most heavily taken, and as these do not start emerging
### Table 1

**Frequency** of Insects by Families Fed to Nestling Purple Martins at Elk Island National Park, Alberta

<table>
<thead>
<tr>
<th>Family</th>
<th>1970 (%)</th>
<th>1971 (%)</th>
<th>Family</th>
<th>1970 (%)</th>
<th>1971 (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aeschnidae</td>
<td>22</td>
<td>27</td>
<td>Coenagrionidae</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Syrphidae</td>
<td>29</td>
<td>17</td>
<td>Muscidae</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Nymphalidae</td>
<td>1</td>
<td>23</td>
<td>Apidae</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>10</td>
<td>4</td>
<td>Cicadellidae</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Siricidae</td>
<td>5</td>
<td>5</td>
<td>Order: Trichoptera</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Formicidae</td>
<td>4</td>
<td>6</td>
<td>Corixidae</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Cerambycidae</td>
<td>5</td>
<td>2</td>
<td>Others</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td>Libellulidae</td>
<td>1</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 Based on percentage of total weight collected (1970, 101.2 g wet weight; 1971, 278.7 g wet weight).

as adults much before the first of August (Can. Dept. Agric. 1958) they were not available for the nestlings studied in 1970. The insignificant difference in biomass of aeschnids (dragonflies) taken is not unexpected because premature death of the nestlings in 1970 biased the food samples towards those families containing small insects that are fed to younger nestlings. The difference in the use of syrphids (flower flies) between the 2 years was significant ($\chi^2$, $P < 0.05$). This seemed to be because syrphid activity is greatly affected by weather conditions. (Under sunny conditions they contributed 24% of diet compared to 3% under cloudy, Spice 1972.) Data from the Edmonton International Airport indicated that 1971 was sunnier (mean hours of sunshine per day 8.7 in 1970 and 12.1 in 1971), drier (total precipitation 11.2 cm in 1970 and 3.1 cm in 1971), and warmer (mean temperature 21.7°C in 1970 and 25.0°C in 1971), so based on weather conditions this difference in use of syrphids between years is not unexpected.

*Influence of time of day on diet.*—The martins' use of various families of insects depended on the time of day the birds were feeding. Of the 4 insect families taken most frequently, aeschnids were captured throughout the day, chironomids (midges) only in the morning, and nymphalids (butterflies) and syrphids mainly around midday (Spice 1972).

To investigate the relationship between time of day and amount of food supplied to nestlings, the rate at which food was supplied was estimated by averaging the weight of food brought per hour for each hour of the feeding period (Fig. 1). I feel that the fluctuation in amount of food brought to the nestlings was a reflection of begging intensity of nestlings, which seemed to influence the number of feeding trips by adults. Begging intensity was higher
in the morning, declined after a feeding period, and cycled in this manner throughout the day. The degree of fluctuation may reflect both the availability of food and the hunger of the adults themselves.

**Influence of nestling age on diet.**—The relative use of various insect families over the nestling period in 1971 is shown in Fig. 2. The size of the insects used in these families (along with their availability) could account for changes in use with age: syrphids <2 cm long, aeschnids and nympha1ids <3 cm long.

**Role of parents in supplying food.**—As nestling age increased, parental feeding increased, and for awhile most of this activity was performed by the male. However, as the need to brood the young decreased, the female provided more food and the male’s proportion of feedings was reduced correspondingly (Spice 1972).

**EFFECTS OF BROOD SIZE**

**Visits to nest.**—A nonproportional increase of adult visits to the nest with increasing brood size has been generally found (Moreau 1939, 1947; Lack
Fig. 2. Use of insect families in relation to age of nestling Purple Martins expressed as % of total food collected for that age. Only those families contributing 10% or more of the weight of food gathered at a specific age are figured. Key to letters above bars: b, Asilidae; d, Coenagrionidae; f, Formicidae; g, Libellulidae; k, Siricidae.
Fig. 3. Mean weight of food samples brought to nestlings by adults throughout the nestling period. Mean brood size in 1970 = 2.5; in 1971 = 3.0.

and Silva 1949; Kendeigh 1952; Gibb 1950, 1955; Morehouse and Brewer 1968; Finlay 1971). However, the assumption that nestlings belonging to larger broods receive less food does not necessarily follow. Adults having larger broods could compensate in several ways to meet their nestlings' energy requirements.

Biomass of food.—One way to compensate would be for the parents of larger broods to bring food samples of relatively greater biomass. To investigate this, the mean weight of each food sample brought per visit was compared with increasing age of nestlings (Fig. 3). In both years mean weight of food brought per feeding trip increased with age; thus the adults were compensating for size of nestlings. However, the data do not indicate a compensation for brood size. The mean values for 1970 were significantly higher than in 1971, but the average brood size in 1970 was 2.5 nestlings compared
Fig. 4. Percentage of nest visits in which adults brought food. Curve fitted by inspection to data from 1970 and 1971. "Small" brood size refers to a brood of 2 nestlings reduced to 1, 19 days post-hatching. "Large" refers to a brood of 4 nestlings reduced to 2, 12 days post-hatching.

To 3.0 in 1971. If the adults were compensating for brood size, food samples should have been heavier in 1971 than in 1970. The difference in mean weight of food samples between the years probably reflected weather conditions, which in 1970 were cooler and cloudier. This was correlated with a greater diversity of prey items in the diet, the majority of these also being smaller items. Two possibilities exist: smaller prey items are coated with more saliva by the adult, thereby increasing the average wet weight recorded per collected sample; or, the adults were collecting a greater total weight of food material per feeding trip when prey items were small in size.

Brood size related to weight of food brought per feeding trip was also investigated using the 1971 data. There was no significant difference in the weights of food samples brought to the 2 broods. Royama's (1966) results differed from mine in that he found average weight of prey brought per feeding trip was heavier among tits feeding smaller broods. This he explained by saying that begging intensity in smaller broods was less and thus gave adults time to select larger prey items. This difference between species may reflect the fact that whereas tits usually bring but one food item per trip, martins frequently bring more than one.
Fig. 5. The effect of brood size on the hourly number of food-bearing visits per nestling Purple Martin. Data from 1971. (See Fig. 4 for explanation of “small” and “large” broods.)

Frequency of feeding trips.—Adults could also compensate for a larger brood by increasing feeding frequency. Figure 4 shows that the percentage of food bearing visits, regardless of brood size, increased with the nestlings’ age. Figure 4 also reveals that adults feeding larger broods carried food on a significantly greater percentage of trips to the nest. This factor has not been considered by many workers who have assumed that all trips to the nest cavity by adults are equal to, or proportionately equal to, the number of food bearing trips.

To determine if this method of compensation gave an individual nestling of the larger brood the same number of actual feedings as those given an individual of the smaller brood, the number of times nestlings were fed per hour was investigated in the 2 broods of different size in 1971 (Fig. 5). Nestlings in the smaller brood were fed significantly more often than were those in the larger brood. Similar results were seen in the data from 1970, but sample size was such that values could only be determined up to day 12.
Daily food intake.—Knowing the mean weight of food brought to the nest per trip and the number of such trips per unit of time for broods of different sizes, it was possible to calculate the total food intake for each brood (Fig. 6). The total weight of food supplied in 1970 was significantly higher than in 1971, probably because of weather conditions, which in 1970 were generally colder than in 1971, and presumably the 1970 nestlings needed more food.

Apparently, food intake of nestlings, per unit time, increased with age to about day 13, and then leveled out (Fig. 6). Results beyond day 18 were not obtained because at this age nestlings began coming to the door to receive food and the adults were able to feed them without activating the recorder.

Nestling growth curves.—Theoretically, nestlings from smaller broods, which received more food per unit of time than did nestlings from larger broods, should exhibit correspondingly different growth curves (Fig. 7). Such seemed to be the case as shown by the data for 1970 and 1971. In each case the smaller brood attained the greatest average individual weight. The difference was not apparent early in nestling life in 1970. This can probably be explained through differential heat loss in different-sized broods. This loss among nestlings of larger broods should be less because of the surface-area-
Fig. 7. Effect of brood size on growth curves. In 1970 broods on the same graph hatched the same day. In 1971 the ‘‘small’’ brood hatched 6 days later than the ‘‘large.’’ ‘‘Small’’ broods had 2 nestlings and ‘‘large’’ had 3.

to-volume relationship, and thus until homeothermy is attained, a larger brood size would be advantageous during a colder season, such as 1970.

Brooding activity.—It has been suggested that, because the surface-area-to-volume ratio is greater for smaller broods, individuals in small broods lose more heat and therefore require more food to maintain themselves than do nestlings of a larger brood size (Royama 1966). It seems possible that increased brooding activity of adults could compensate for this to some extent. Amount of time spent not brooding by females with small and large broods was analyzed for 1971 (Fig. 8). The percentage of time nestlings were brooded decreased with age to day 16 or 17, after which females ceased brooding. Slopes of regression lines were similar for both brood sizes, however, percent of time spent brooding the larger brood was significantly less than that spent brooding the smaller. Royama (1966) found a similar situation among Great Tits (Parus major). This suggests that the parents do reduce heat loss by their nestlings through brooding behavior. This observation has general implications for clutch size. Adults with a small brood can more
Fig. 8. Brood size related to percentage of time nestling Purple Martins were not brooded throughout the nestling period. Data from 1971. Regression lines: Large, \( Y = 8.9 + 5.8X \); Small, \( Y = -10.1 + 6.1X \).

easily provide them with food and intensive brooding. As brood size increases, and the surface-area-to-volume relationship decreases, heat loss by nestlings decreases. Thus, although adults must spend more time feeding young in large broods they can accomplish this by spending less time brooding. Hence, for any particular year there is an optimum brood size that permits adults to feed and brood the young with greatest success; beyond this brood size sur-
vival of nestlings declines. It is this optimum brood size, which varies from year to year depending on weather conditions that probably determines what the mean clutch size will be for an area.

SUMMARY

A study of the food of nestling Purple Martins at Elk Island National Park, Alberta, during the summers of 1970 and 1971 indicated that insects of the families Syrphidae, Nymphalidae, and Aeschnidae comprised the majority of their diet. The quality and quantity of food fed to the nestlings changed with season, time of day, and age of nestlings.

The influence of brood size was investigated to see if adults were compensating for the energy requirements of a larger brood in ways other than increasing the number of visits to the nest. They did not bring a greater biomass of food per feeding trip. They did increase the percentage of trips to the nest that were feeding trips, but, in spite of this, individual nestlings from smaller broods were fed more often than those from larger broods. This was reflected in nestling growth curves in which nestlings of smaller broods attained a greater weight prior to fledging. Adults with larger broods spent less time brooding nestlings than did adults with smaller broods, possibly a result of a smaller surface-area-to-volume ratio, and consequently lesser heat loss by nestlings in larger broods.

ACKNOWLEDGMENTS

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REPRODUCTION AND NEST SITE SELECTION BY 
RED-WINGED BLACKBIRDS IN NORTH LOUISIANA

BRYAN T. BROWN AND JOHN W. GOERTZ

The purposes of this study were to investigate reproductive variations and nest site selection of Red-winged Blackbirds (*Agelaius phoeniceus*) in primarily upland habitat in north Louisiana. This study provides further information on the nesting ecology of the Red-wing and research that is necessary in compiling an accurate picture of Red-wing population ecology throughout North America, as stressed by Gottschalk (1967). In addition, knowledge of local breeding populations is important, since most blackbird damage to rice is done by resident birds (Meanley 1971).

STUDY AREA AND METHODS

Most nests were found in Lincoln Parish, Louisiana, although significant numbers were found in other portions of north Louisiana within an area delimited by the borders of Texas and Arkansas, the Ouachita River, and the city of Alexandria. The study area, referred to as the Northwest Louisiana Uplands (St. Amant 1959), is generally hilly with elevations ranging from 15 to 161 m above sea level. A few rivers traverse the area, but most streams are small and slow-moving, subject to rapid rises and flooding. After reforestation, much of the area has developed a heavy second growth of native pines and hardwoods. The clearing of these forested areas along streams to provide pastures for cattle, man-made reservoirs, and small farm ponds has increased available Red-wing nesting habitats.

A total of 755 Louisiana Tech University museum record cards for active nests from 1963 to 1975 were available for analysis. Although some nests, represented by nest cards, were originally located by undergraduate ornithology students, all nests were checked (authenticated) one or more times by at least 1 of us or by ornithology graduate students who had previously conducted nest studies. In some instances observations denoted on the cards were incomplete. This is, in part, the reason for the variations in numerical totals for different categories of data.

During each of the annual nesting seasons a rather equal amount of time and effort was allotted to an overall search for nests, eggs, young, and related data. However, some types of data were collected only during 1975; these are so indicated when presented.

Various clues suggested the predators responsible for a nest loss. Eggshells present around the nest site indicated a mammalian predator. Loss of 1 or 2 eggs possibly indicated an avian predator, as did the presence of "peek holes." Snakes and mammals usually ate all eggs in a nest. Robertson (1972) stated that egg loss in nests not accompanied by significant nest damage was due to snakes or birds.

The season was divided into 2-week periods for the purpose of data analysis. Nests containing completed clutches that were discovered during the first 5 days of a 2-week period were considered to have been active during the immediately preceding period; as were nests with young. Those nests found that contained eggs during the first 5 days of a 2-week period were assumed to have been built in the preceding period; nests that contained young on the first 5 days of a period were assumed to have been built 2 periods
Table 1

Chronology of Nesting as Indicated by the Observed Number of Active Nests, Eggs, and Young Present in 2-week Periods, 1963 to 1975

<table>
<thead>
<tr>
<th>Category</th>
<th>April 1-15</th>
<th>April 16-30</th>
<th>May 1-15</th>
<th>May 16-31</th>
<th>June 1-15</th>
<th>June 16-31</th>
<th>July 1-15</th>
<th>July 16-31</th>
<th>August 1-15</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of active nests</td>
<td>2 102</td>
<td>535 243</td>
<td>102 58</td>
<td>23 6</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of eggs</td>
<td>7 181</td>
<td>1405 522</td>
<td>181 148</td>
<td>40 14</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of young</td>
<td>4 303</td>
<td>211 99</td>
<td>85 39</td>
<td>7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

previously. Nest building time was assumed to take 6 days (Bent 1958). Young per nest calculations are based on nests containing young, and not on total nests.

Only those eggs actually observed were included in the total number of eggs, including known unhatched eggs, but eggs as indicated by eggshells were not included. A complete clutch was one in which 2, 3, 4, or 5 eggs were successively counted during successive observations. Certain eggs were measured at random throughout the 1975 season with a Vernier beam caliper. If both eggs and young were present, the date the eggs were laid was calculated by adding the age of the young (Bent 1958, Holcomb and Twist 1971) to the incubation period of 10 to 12 days (Allen 1914). The number of eggs and young present during 2-week periods was determined by tallying only the number of eggs of young observed during the period.

Results and Discussion

Active nests with eggs were present from 7 April to 2 August (Table 1). Similarly, they occurred from 7 April to 23 August in Arkansas (Meanley 1971) and 30 April to 6 August in Ohio (Dolbeer 1976). The largest number of active nests occurred during the first half of May as were those recorded by Smith (1943) in Illinois. Elsewhere, the height of the nesting season occurred later: mid May in Ohio (Dolbeer 1976), late May in Connecticut (Robertson 1973) and New York (Allen 1914, Case and Hewitt 1963) among marsh nesters, but seems to occur in early June among upland nesters in New York.

Inactive nests were not tallied prior to 1975, but in 1975, 24 of 151 nests (16%) followed from the time nests were built were found in which no eggs or young were known to have been present; some of these may have been victims of snake predation. Bent (1958) and Goddard and Board (1967) found that many completed Red-wing nests were never used.

Of 2178 eggs recorded, 1461 made up 382 known completed clutches, for an average of 3.82 (range, 2-5) eggs per clutch. Two completed clutches had 2 eggs; 73, 3 eggs; 297, 4 eggs; and 10, 5 eggs. This was higher than
the average number of eggs reported by Robertson (1973) in Connecticut (3.37 to 3.50); by Dolbeer (1976) in Ohio (3.38); by Beer and Tibbits (1950) in Wisconsin (3.7); by Orians (1961) in California (3.45 to 3.75); or by Meanley (1971) on the Arkansas Grand Prairie (3.2). Incubation usually begins after the third egg is laid (Bent 1958). But, in this study, many nests containing only 3 eggs were not included as completed clutches due to insufficient observations. If all clutches containing 3 or more eggs are included as completed clutches, then, average clutch size for this study is 3.66.

Bent (1958) reported that the range of eggs per completed clutch was 3 to 5. Goddard and Board (1967) in Oklahoma, and Case and Hewitt (1963) in New York found 1 to 5 eggs per clutch, while Orians (1961) in California found 1 to 6, and in this study, as well as Dolbeer’s (1976), the range was 2 to 5. We found 2 nests in which there were 2 known eggs, laid, incubated, hatched and young successfully fledged. It is possible that some eggs were removed from these nests by predators or cowbirds or accidentally ejected. Since the active periods for these 2 nests were late June and early July it is also possible that these were second broods or renesting attempts. Double brooding (Meanley 1971), or renesting attempts is common (Smith 1943, Bent 1958, Goddard and Board 1967, Dolbeer 1976). Goddard and Board (1967) reported that clutch size does decrease later in the nesting season and Dolbeer (1976) found 2-egg clutches common late in the season in Ohio.

During the earliest and latest parts of the nesting season, clutches of 3 eggs were most common, whereas clutches of 4 eggs were most common during the peak of the nesting season (Table 2). Clutches containing 5 eggs were present only during the height of the nesting season.

The incubation period was 11 to 13 days. There were 36 known unhatched eggs among incubated clutches, 25 of which were recorded in 1975 when careful observations were made for this detail.

Average egg size of 303 eggs was 17.4 × 23.6 mm. Egg width ranged from 15.9 to 18.8 mm, whereas length ranged from 21.0 to 28.1 mm. Egg size was similar to the average of 17.5 × 24.8 mm for 300 eggs in the United States National Museum (Bent 1958). The lower range in both egg length and width is approximately the size of eggs laid by the Brown-headed Cowbird (this study and Bent 1958). There were no notable variations in egg size as the season progressed. Statistical analysis of average egg sizes seasonally showed no significant difference to exist (t-test, P > .05).

Nests were found in 30 species of plants, as compared to 30 in New York (Case and Hewitt 1963); 30 in Florida (Stowers et al. 1968); and 70 in Arkansas (Meanley 1971). Major Plant types used for nest support were buttonbush (Cephalanthus occidentalis), willow (Salix spp.), rush (Juncus
Table 2
Maximum Number of Eggs Known per Nest During 2-week Periods, 1963 to 1975

<table>
<thead>
<tr>
<th>Number of eggs per nest</th>
<th>April</th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>August</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a</td>
<td>b</td>
<td>a</td>
<td>b</td>
<td>a</td>
</tr>
<tr>
<td>1</td>
<td>8</td>
<td>39</td>
<td>14</td>
<td>11</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>8</td>
<td>55</td>
<td>10</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>23</td>
<td>191</td>
<td>56</td>
<td>23</td>
</tr>
<tr>
<td>4</td>
<td>1</td>
<td>22</td>
<td>214</td>
<td>71</td>
<td>17</td>
</tr>
<tr>
<td>5</td>
<td>7</td>
<td>2</td>
<td>2</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Average number of eggs per nest: 3.5 3.0 3.2 3.1 2.8 2.6 2.7 3.0 2.5

spp.) bulrush (*Scirpus cyperinus*), cattail (*Typha* spp.), common alder (*Alnus serrulata*), sweetgum (*Liquidambar styraciflua*), dock (*Runicex* spp.) and grasses (*Graminae*) (Table 3). Plants of minor importance (used 1 to 9 times) were pine (*Pinus* spp.), cypress (*Taxodium* sp.), silverling (*Baccharis halimifolia*), vasey-grass (*Paspalum urvillei*), privet (*Ligustrum sinense*), wax-myrtle (*Myrica cerifera*), peach (*Prunus persica*), horse-chestnut (*Aesculus pavia*), oak (*Quercus* spp.), live-oak (*Quercus virginiana*), common elder (*Sambucus canadensis*), ironweed (*Vernonia* sp.), hawthorn (*Crataegus* spp.), redbud (*Cercis canadensis*), rose (*Rosa* sp.), sassafras (*Sassafras albidum*), blackberry (*Rubus* sp.), sumac (*Rhus* sp.), thorough-

Table 3
Season Use of Plant Species for Nest Support by Red-winged Blackbirds*

<table>
<thead>
<tr>
<th>Supportive plant</th>
<th>April</th>
<th>May</th>
<th>June</th>
<th>July</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a</td>
<td>b</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>Buttonbush</td>
<td>**</td>
<td>75</td>
<td>104</td>
<td>28</td>
</tr>
<tr>
<td>Willow</td>
<td>1</td>
<td>20</td>
<td>46</td>
<td>3</td>
</tr>
<tr>
<td>Rush</td>
<td>**</td>
<td>16</td>
<td>23</td>
<td>2</td>
</tr>
<tr>
<td>Bulrush</td>
<td>1</td>
<td>7</td>
<td>3</td>
<td>11</td>
</tr>
<tr>
<td>Cattail</td>
<td>1</td>
<td>9</td>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td>Common Alder</td>
<td>1</td>
<td>9</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Sweetgum</td>
<td>3</td>
<td>8</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Dock</td>
<td>5</td>
<td>9</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Grasses</td>
<td>1</td>
<td>10</td>
<td>30</td>
<td>1</td>
</tr>
</tbody>
</table>

** Nests not observed but probably did occur.
TABLE 4
HEIGHTS OF 393 RED-WINGED BLACKBIRD NESTS, LISTED BY HABITAT TYPE

<table>
<thead>
<tr>
<th>Habitat</th>
<th>No. of plant species used</th>
<th>No. of nests</th>
<th>Ave. height of nests in m (range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>FRESHWATER AREAS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seasonally flooded basins (ditches, etc.)</td>
<td>9</td>
<td>117</td>
<td>1.2 (0.3-3.1)</td>
</tr>
<tr>
<td>Open freshwater areas (edge)</td>
<td>15</td>
<td>173</td>
<td>1.0 (0.2-4.0)</td>
</tr>
<tr>
<td>UPLAND AREAS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pasture (edge)</td>
<td>15</td>
<td>78</td>
<td>1.4 (0.3-7.6)</td>
</tr>
<tr>
<td>Cultivated areas (orchards, arboretum, etc.)</td>
<td>8</td>
<td>25</td>
<td>1.1 (0.2-3.0)</td>
</tr>
<tr>
<td>TOTALS</td>
<td>29</td>
<td>393</td>
<td>1.1 (0.2-7.6)</td>
</tr>
</tbody>
</table>

1. Habitat types from Shaw and Fredine (1956).

wort (Eupatorium perfoliatum), persimmon (Diospyros virginiana) and cornel (Cornus foemina).

Of 554 nest sites for which the plant species was known, 261 (47%) were in buttonbush, a common hydrophilic shrub of marshes, lakes, and low pastures throughout the Southeast. Stowers et al. (1968) found buttonbush to comprise 28% of the plants used for nesting by the Red-wing in Florida. Cattail (90%) and willow (4%) comprised the majority of supportive plants used in Oklahoma (Goddard and Board 1967), whereas Robertson (1972) found cattail and dock to be the most used plants in Connecticut.

Variation in the average height of Red-wing nests within different habitats is shown in Table 4. The ratios of plants used changed from one habitat to another, as did plant occurrence (Table 4). In addition, the height of nests occurring in single plant species may differ with a change in habitat. On upland sites, it appeared to Francis (1973) that nest site selection was independent of height above the ground, but was related to the distance below the top of the vegetative canopy. Heights may be associated with the changing growth form of plants dictated by different environmental conditions in each habitat. Most nests tended to be lower when over open water, and higher when over seasonally flooded basins or pastureland (Table 4), although this was not always true. The largest number of nests occurred in open freshwater areas: possibly indicating that open freshwater is the preferred habitat in north Louisiana. A pooled t-test analysis of nesting habitats and nest heights (Table 4) indicates that a very highly significant difference in nest height existed between the 2 freshwater areas (P < .001). In addition,
a significant difference (P < .05) existed between upland and freshwater areas. Lesser differences were noted between upland habitats (P < 0.10).

Nesting success was compared with nest height (Table 5), depth of water below the nest (Table 6), and among the 6 major supportive plant types (Table 7).

From 1963 to 1975, 65 known successful nests were recorded. A more valid comparison of successful nests is given by careful observations made during 1975: 35 known successful (23.1%) nests and 9 probably successful (5.9%) out of 151. However, if only active nests are compared, 44 of 127 (35%) were successful, compared with 43% reported by Bent (1958), 29% in Wisconsin (Young 1963), 32% in New York (Case and Hewitt

### Table 5

<table>
<thead>
<tr>
<th>Height (m)</th>
<th>Number of nests</th>
<th>Number successful</th>
<th>Percent successful</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0-0.6</td>
<td>16</td>
<td>2</td>
<td>12.5</td>
</tr>
<tr>
<td>0.6-1.2</td>
<td>32</td>
<td>9</td>
<td>28.1</td>
</tr>
<tr>
<td>1.2-1.8</td>
<td>43</td>
<td>14</td>
<td>32.5</td>
</tr>
<tr>
<td>1.8-2.4</td>
<td>21</td>
<td>7</td>
<td>33.3</td>
</tr>
<tr>
<td>2.4-8.0</td>
<td>14</td>
<td>3</td>
<td>21.5</td>
</tr>
<tr>
<td>Totals</td>
<td>126</td>
<td>35</td>
<td>27.8</td>
</tr>
</tbody>
</table>

### Table 6

<table>
<thead>
<tr>
<th>Depth of water under nest (cm)</th>
<th>Number of nests</th>
<th>Number successful</th>
<th>Percent successful</th>
</tr>
</thead>
<tbody>
<tr>
<td>127 ACTIVE NESTS (1975)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>76</td>
<td>24</td>
<td>35.1</td>
</tr>
<tr>
<td>1-15</td>
<td>39</td>
<td>7</td>
<td>17.9</td>
</tr>
<tr>
<td>over 15</td>
<td>12</td>
<td>4</td>
<td>33.3</td>
</tr>
<tr>
<td>totals</td>
<td>127</td>
<td>35</td>
<td>27.6</td>
</tr>
<tr>
<td>ISOLATED BREEDING POPULATION (1975)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>25</td>
<td>11</td>
<td>44.0</td>
</tr>
<tr>
<td>1-15</td>
<td>9</td>
<td>3</td>
<td>33.0</td>
</tr>
<tr>
<td>over 15</td>
<td>8</td>
<td>4</td>
<td>50.0</td>
</tr>
<tr>
<td>totals</td>
<td>42</td>
<td>18</td>
<td>43.0</td>
</tr>
</tbody>
</table>
1963), 50% in Maryland (Frankhauser 1964), and 53% in Pennsylvania (Brenner 1966). Nesting success of this study may be small due to individual breeding populations covered in this analysis having been relatively small compared to larger breeding populations that are often reported in extensive marshes. In larger nesting colonies, predation pressure per individual nest is much lower than in small colonies (Darling 1938, Fautin 1941, Smith 1943, Robertson 1973). However, in this study, an upland breeding population of 42 nests had 43% success in 1975, a slightly higher success rate than all other nests combined for that year (Table 6).

We observed 685 young in 239 nests for the average of 2.87 (range, 1–5) young per nest. An average of 2.77 young per nest were fledged from the 65 successful nests, from 1963 to 1975. For the 1975 season alone, 2.97 young were known fledged per successful nest. The average number of young fledged per active nest (N = 127) in 1975 was 0.33. This compares to 0.6 in New York (Case and Hewitt 1963), and as high as 1.9 in Ohio (Francis 1975). Dolbeer (1976) reported the average number of young fledged annually per female as 1.3 in Ohio. In this study, young were present from 25 April to 23 July, with the largest number of young recorded in early May (Table 1).

Meanley (1971) reported that nesting success was higher in nests more than 0.6 m above the ground, while Goddard and Board (1967) noted that lower nests were more successful; however, the majority of those nests were over water in cattails. Data in Table 5 indicate that nests in the 1.2 to 1.8 m range and 1.8 to 2.4 m range were similarly successful (32.5% and 33.3%) and nests at 0.6 to 1.2 m were only slightly less successful (28.1%). Low success (12.5%) for nests 0 to 0.6 m high was due, largely, to predation. The highest nests (over 2.4 m) were not necessarily the most successful (21.5%). This may have been due to weather factors, e.g., those nests knocked down by wind and rain (Francis 1971). Goddard and Board (1967) and Robertson (1972) observed that nesting success was greater as the depth of the water below the nest increased. The smaller number of nests over deep water were as successful (33.3%) as all the combined nests over land (31.5%) (Table 6). The nests over shallow water (1 to 15 cm) had poor nesting success (17.9%). This may be due, in part, to the fact that nests over water tend to be lower (Table 4), whereas the shallow water would not afford the protection of nests over deeper water (Table 6).

Nesting success is also partially related to sturdier vegetation forms which adequately support nests through periods of severe weather (Francis 1971). Buttonbush and bulrush were the most commonly used supportive plants and nests placed in these plants also had relatively high success, 32% and 26%, respectively, of all successful nests (Table 7). The grouping of all other
Supportive Plant Type and Nesting Success for 127 Active Nests in 1975

<table>
<thead>
<tr>
<th>Supportive Plant</th>
<th>Number of nests</th>
<th>Number known successful</th>
<th>Percent successful</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buttonbush</td>
<td>50</td>
<td>16</td>
<td>32</td>
</tr>
<tr>
<td>Willow</td>
<td>7</td>
<td>1</td>
<td>14</td>
</tr>
<tr>
<td>Rush</td>
<td>12</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>Bulrush</td>
<td>23</td>
<td>6</td>
<td>26</td>
</tr>
<tr>
<td>Cattail</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Common Alder</td>
<td>13</td>
<td>3</td>
<td>23</td>
</tr>
<tr>
<td>Others</td>
<td>17</td>
<td>8</td>
<td>47</td>
</tr>
<tr>
<td>Totals</td>
<td>127</td>
<td>35</td>
<td>28</td>
</tr>
</tbody>
</table>

seldom-used plants had a rather high success (47.1%); the reason for which is not clearly understood. Robertson (1972) also observed a relatively high success in rarely-used upland woody vegetation. He suggested that these favorable nesting sites are not used more often because they are poorly suited for the grouped territorial nesting pattern to which Red-wings are adapted.

Only 174 (22%) known unsuccessful nests were recorded out of 755 active nests, from 1963 to 1975, compared to 82 (65%) unsuccessful nests recorded out of 126 carefully observed active nests in 1975. In 1975, 88 instances of predation occurred on the 82 nests. Nest losses not accompanied by significant nest damage, an indication of probable snake or bird predation, were most common (56 of 88 occurrences) throughout the nesting season. Mammalian predators played a lesser role (27); whereas weather (3) and mowing or grazing (2) were rather insignificant contributors to lack of nesting success.

Other losses can be attributed to the Brown-headed Cowbird (Molothrus ater). Smith (1943) found the incidence of parasitism by the Brown-headed Cowbird to be from 5% (1940) to 0.6% (1941) for the same location. We found 12 of 755 (1.6%) active nests were parasitized from 1963 to 1975. Sixteen cowbird eggs were laid, including 1 nest with 3 cowbird eggs, 2 nests with 2 eggs, and 9 nests with 1 egg. In the 12 parasitized nests, an average of 2.2 (range, 1-4) Red-wing and 1.3 cowbird eggs were present. Cowbird eggs were found in Red-wing nests from 30 April to 29 May at heights of 1 to 2.5 m in a wide range of supportive plants in all the major habitat types. The cowbird laying peak seemed to coincide with the peak laying period of the Red-wing (Goertz 1977). In 1975, 2 cowbird eggs were measured, being $15.8 \times 20.8$ mm and $16.4 \times 19.8$ mm, only slightly smaller than Red-wing eggs.
SUMMARY

Data were collected on 755 active nests of the Red-winged Blackbird (Agelaius phoeniceus) in a largely forested area of north Louisiana from 1963 to 1975. Nesting began in early April and continued until early August; the height of the nesting season was during May. Completed clutches contained an average of 3.82 eggs (range, 2 to 5); broods contained an average of 2.87 (range, 1 to 5) young. During 1975, 0.83 young fledged per nest for 127 active nests.

Thirty species of plants were used as nest sites, with the ratios of plants used being different in each of the 4 major habitats. Average nest height varied with the habitat in which the nest was located. Open freshwater areas were the most heavily used habitats. Nesting success was directly related to the height of the nest, depth of water below the nest, type of vegetation used for nest support, and nesting habitat. Predation was a major factor involved in nest loss.

ACKNOWLEDGMENTS

We are grateful to James G. Dickson and John L. Murad for assistance during certain phases of this work, to Donald G. Rhodes for help in plant identification, to John E. Carothers for help in making statistical comparisons, to many students who helped in locating nests, and to Richard A. Dolbeer. Brooke Meanley. and Raleigh J. Robertson for their review of this manuscript.

LITERATURE CITED


DEPT. OF ZOOLOGY, LOUISIANA TECH UNIV., RUSTON 71272. ACCEPTED 15 DECEMBER 1976.
THE RUFOUS-COLLARED SPARROW AS A HOST OF THE SHINY COWBIRD

ROSENDO M. FRAGA

The Rufous-collared Sparrow or Chingolo (Zonotrichia capensis) is one of the main hosts of the Shiny Cowbird (Molothrus bonariensis) through most of their overlapping range in South America. The most recent study on the interaction between these species was carried out by King (1973) in Horco Molle, province of Tucumán, northwestern Argentina.

In 1970 I began to collect data on all the nests of Rufous-collared Sparrows which I found in my study area near Lobos, province of Buenos Aires, Argentina. Rufous-collared Sparrows are quite abundant here and I have found 45 nests. The data reported here relating to the interaction between host and brood parasite differ from data collected from Tucuman by King (1973), and also from the data collected near Rio de Janeiro, Brazil, by Sick and Ottow (1958; original not seen: their observations are extensively quoted in the paper of King). My data are also relevant to other studies on the brood parasitism of the Shiny Cowbird which I am carrying out in the same study area. One of these studies, begun in 1972, is centered on the reproductive interactions of the Shiny Cowbird and the Chalk-browed Mockingbird (Mimus saturninus). I think that only comparative studies will throw light on some aspects of the breeding biology of the Shiny Cowbird, such as the significance of the polymorphism in egg shell color.

Since 1969 I have also been studying the breeding of the Bay-winged Cowbird or Bay-wing (Molothrus badius) and its brood parasite the Screaming Cowbird (Molothrus rufoaxillaris). I have already published a short preliminary account on both species (Fraga 1972). Since I began this study I have found an increasing number of nests of Bay-wings parasitized by both the Screaming and the Shiny cowbirds. This situation seems to have been overlooked and was only briefly commented on by Friedmann (1929:119), although among other things it is an additional complication to the problem of the proper identification of the eggs found in the nests of Bay-wings.

STUDY AREA AND METHODS

All the nests of sparrows were studied in the main woodland of Estancia La Candelaria, Lobos, Province of Buenos Aires, Argentina (about 35° 15′ S) and in 2 smaller adjacent wooded areas. Between 1970–1972 I found most nests in a small woodland of about 0.8 ha, fenced off from the surrounding pasture with barbed wire (the fenced area is about 1
ha). The most abundant trees are the North American locusts *Robinia pseudoacacia* and *Gleditsia triacanthos*, and the native tala (*Celtis spinosa*). As this area is protected from grazing cattle and horses, young trees and saplings are quite numerous. From September to early January there is a rich cover of tall grasses, chiefly *Bromus unioloides*. From 1972 onwards most nests were found in the main woodland of La Candelaria, a more complex area which covers about 80 ha. Basically this area includes a central zone of gardens, orchards, and lawns surrounded by a belt of untended dense woodland where several species of trees, shrubs, palms, and vines have become naturalized. In these years I have also studied some nests in a hedgerow of native trees and shrubs (*Celtis spinosa*, *Parkinsonia aculeata*, and *Sambucus australis*) bordering a drainage ditch.

All nests were found along routes or in places which I visited frequently, often daily, for the study of other birds. The sample of 45 nests could be divided into 2 subsamples. The first comprises 40 nests which were found only with eggs of sparrows or cowbirds or of both species. In this subsample only 7 nests were found in or before the egg-laying period of the sparrows, as new sparrow eggs were laid after my first visit. The remaining 33 nests were found during the incubation period of the sparrows. The second subsample comprises 5 nests which were found with at least one nesting sparrow or cowbird. The inclusion of this subsample in the computations of nesting success would overstate success. My experience with both species suggests that non-parasitized nests have a higher chance of reaching the nestling or fledgling stage than parasitized ones. For this reason this subsample will be excluded from computations on the incidence of parasitism.

Once found, all the nests of sparrows were visited either daily or at 2-day intervals. All the eggs and the younger nestlings were marked; older nestlings were banded with colored celluloid bands. Day 0 designates the day in which the nestlings hatched, and day 1 is the following day. Nestlings were usually weighed around noon.

**THE LOCAL HOSTS OF THE SHINY COWBIRD**

Broadly speaking we have good general information on the species of passerines parasitized by Shiny Cowbirds in this part of Argentina (Friedmann 1929, 1963) though more intensive studies are needed. In 8 years of bird study in La Candelaria I have found eggs of Shiny Cowbirds in the nests of 12 species of passerines. About 33 species of passerines breed regularly here, but my coverage for some species breeding exclusively in open country or in marshes is not good. Most of my nesting records (more than 350 up to 1975) are of the 24 species of passerines that breed in wooded areas. In this group I have found eggs of Shiny Cowbirds in the nests of the following 8 species: Cattle Tyrant (*Machetornis rixosus*), Fork-tailed Flycatcher (*Muscivora tyrannus*), Tropical Kingbird (*Tyrannus melancholicus*), House Wren (*Troglodytes aedon*), Chalk-browed Mockingbird, Rufous-bellied Thrush (*Turdus rufiventris*), Bay-winged Cowbird, and Rufous-collared Sparrows. More than 50% of the nests of the Fork-tailed Flycatchers, mockingbirds, and sparrows were parasitized. I paid particular attention to the local species recorded as effective hosts (rearing fledgling cowbirds) by Friedmann (1963:197), such as the Rufous Hornero (*Furnarius rufus*) and
the Masked Gnatcatcher (*Polioptila dumicola*); for these species I have no local records of parasitism.

Although this list could eventually be enlarged, the important point is that it is unlikely that any of the remaining 16 species could be an important effective host of the Shiny Cowbird. This is also shown by the following list of 6 species of woodland birds that have been recorded rearing fledglings of Shiny Cowbirds in La Candelaria between 1970–1975: Cattle Tyrant (1 record), Fork-tailed Flycatcher (no less than 14 records), Tropical Kingbird (2 records), House Wren (4 records), Chalk-browed Mockingbird (6 records), and Rufous-collared Sparrows (12 records excluding those reported here). The lack of records for the Rufous-bellied Thrush may simply reflect the fact that it is a scarce bird in my study area; the peculiar situation of the Bay-wing needs another explanation.

**BREEDING BIOLOGY OF RUFOUS-COLLABRED SPARROWS**

Rufous-collared sparrows are resident throughout the year in La Candelaria. Some males may show sporadic outbursts of territorial behavior (including singing) in early August in periods of fair weather, but I have not detected nesting activities at such early dates. Sustained territorial behavior can be observed from late August to early February.

My earliest record of a nest-building female is 16 September (1975) in the main woodland. Table 1 shows the number of nests of sparrows by periods of half months. The start of egg-laying was known or could be calculated in 22 nests. The remaining 23 nests are placed in the table in the period in which they were found. In my sample the earliest date for egg-laying was 22 September 1975 (calculated). The latest nest (with eggs) was found on 11 February 1971.

In La Candelaria all the nests of sparrows which I found were built on or near the ground. The highest nest was built 12 cm above ground level in a tangle of the vine *Doxantha unguis-cati* growing over a casuarina tree. Most nests were built in dense cover and near the bases of trees, fallen branches, or protruding roots. Otherwise there was considerable variation in the location and degree of exposure of the nest. In places with a sparse ground cover, such as dense woodland, nests were often found under piles of fallen branches. Some peculiar locations include 2 nests built inside low, open hollow stubs (both parasitized), another built in a cavity at the base of a tree, 2 nests built in deep niches in the slopes of a drainage ditch (1 parasitized), and one nest found under the concave side of the basal sheath of a fallen palm frond (parasitized). Some nests were completely covered from above.

As most local passerines, Rufous-collared Sparrows lay either 3 or 4 eggs. The mean clutch size of 11 non-parasitized nests was 3.18 eggs; there
Table 1

Temporal Distribution of Nests of Rufous-collared Sparrows, by Periods of Half-Months*

<table>
<thead>
<tr>
<th>Period</th>
<th>Parasitized nests</th>
<th>Non-parasitized nests</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>15-30 September</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>1-15 October</td>
<td>3</td>
<td>-</td>
<td>3</td>
</tr>
<tr>
<td>16-31 October</td>
<td>4</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>1-15 November</td>
<td>5</td>
<td>3</td>
<td>8</td>
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<tr>
<td>16-30 November</td>
<td>8</td>
<td>4</td>
<td>12</td>
</tr>
<tr>
<td>1-15 December</td>
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<td>4</td>
</tr>
<tr>
<td>16-31 December</td>
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<td>-</td>
<td>1</td>
</tr>
<tr>
<td>1-15 January</td>
<td>5</td>
<td>-</td>
<td>5</td>
</tr>
<tr>
<td>16-31 January</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>1-15 February</td>
<td>-</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>TOTAL</td>
<td>31</td>
<td>14</td>
<td>45</td>
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</tbody>
</table>

* Five nests found in the nestling period are included in the table.

were 9 nests with 3 and 2 nests with 4 eggs. Of the 3 non-parasitized nests found in the nestling stage, 2 contained 3 nestlings and the other 4 nestlings. A comparison with the data assembled by King (1973: Table 1) shows the expected gradual increase in clutch size with latitude (2.69 eggs in Tucuman and 2.31 eggs in Rio de Janeiro).

Measurements of 32 eggs of Rufous-collared Sparrows were as follows: range 16.4–21.8 × 13.5–15.9 mm; mean and standard error: 19.28 ± 0.23 × 14.76 ± 0.09 mm.

The incubation period could only be determined in one nest with 3 eggs, and was 13 days. In this nest the first 2 eggs hatched on day 12, but the spread of hatching was less than 24 h.

Nestlings were fed insects by both parents. By day 2 the nestlings may partially open their eyes when begging food: this becomes more noticeable at day 3. By day 6 pinfeathers begin to emerge. The nestling period of Rufous-collared Sparrows was 9–11 days (7 nestlings). At day 8 nestlings may attempt to leave the nest.

Three banded fledglings remained in the parental territory for at least 19 days. They were fed at first by both parents, later probably chiefly by the male. At this time (15 December 1974) the female was apparently attending a second nest which I was unable to locate.

These observations suggest that Rufous-collared Sparrows may attempt 2 or even 3 broods in a season, but with their low nesting success probably few pairs will succeed in raising more than one brood.
THE BREEDING SEASON AND NEST-SEARCHING BEHAVIOR OF SHINY COWBIRDS

In La Candelaria, Shiny Cowbirds can be seen in variable numbers throughout the year. As I have but a few banded individuals, I know little about their local movements. Outside the breeding season they come to the main woodland only for roosting. The largest flocks can be seen in winter.

In my sample of parasitized sparrow nests the earliest date for eggs of Shiny Cowbirds was 26 September 1975. This is the earliest date I have for cowbird eggs in the nests of any host. The latest parasitized nest of sparrow was found on 27 January 1972; I have 2 unquestionable later records of parasitism by Shiny Cowbirds in 2 nests of Bay-wings: 2 immaculate white eggs were laid on 5 and 7 February 1975. The overlap in the breeding seasons of Rufous-collared Sparrows and Shiny Cowbirds was 87% in my sample but this figure is probably a minimal estimate of the actual overlap.

I have 14 records of female Shiny Cowbirds watching the movements of Sparrows. Twice I had already seen a nest of sparrow in the area; one of these nests was parasitized the following day. The female cowbirds were watching the movements of the sparrows from some convenient perch. At times they uttered chattering notes, particularly when they flew away. On 11 October 1970 while I was watching a nest-building female sparrow, I observed a female cowbird that remained no less than 17 min doing the same from a nearby branch. Then she alighted near the nest but soon flew away while the female sparrow was chipping. This nest was never finished. Twice 2 female cowbirds were seen searching in the same area at the same time.

Only twice did I observe male Shiny Cowbirds that followed nest-searching females as they moved away. This does not necessarily mean that they were helping the females in any way. In my opinion most records in the earlier literature, particularly in Hudson (1920 I:75) of male Shiny Cowbirds visiting nests of other birds with females in this part of Argentina were probably caused by confusion with male Screaming Cowbirds. As I will show in my account on the species, pairs of Screaming Cowbirds not only visit nests of their hosts, the Bay-wings, but also nests of other birds. I have no records of Screaming Cowbirds visiting nests of Rufous-collared Sparrows.

INCIDENCE OF PARASITISM

In my sample of 40 nests found either during the egg-laying or the incubation period of the sparrows, 29 (72.5%) nests were parasitized. In the additional sample of 5 nests found in the nestling period, 2 nests were parasitized.

A seemingly significant difference between my observations and those re-
ported by King (1973) from Horco Molle can be observed in the temporal distribution of non-parasitized nests. At Horco Molle both host and parasite have slightly longer breeding seasons with an overlap of 87%. Although the overall incidence of parasitism was perhaps lower than in my study area (66% vs 72.5% in the sample of 40 nests, or vs 69% in the sample of 45 nests but difference not significant), at the peak of the breeding season of the sparrows all their nests (100%) were parasitized. As can be seen in Table 1, in my study area non-parasitized nests were more evenly distributed throughout the breeding season of the sparrows and even at the peak of their breeding season (period 15 October–15 January) only 27 out of 35 nests (77.1%) were parasitized.

SEQUENCE OF EVENTS IN FIVE PARASITIZED NESTS

Of the 7 nests found in or before the egg-laying period, 5 nests were parasitized in the following way:

Nest 11: 27 October 1972, found with sparrow egg; 28 October 1972, this sparrow egg was removed, now one sparrow egg plus 2 cowbird eggs (1 immaculate, 1 spotted); 29 October, now 2 sparrow eggs plus 4 cowbird eggs (2 immaculate, 2 spotted); 30 October, 2 sparrow eggs (number 3 punctured) plus 5 cowbird eggs (3 immaculate, 2 spotted) but nest abandoned, all the eggs were cold. The nest retained all its contents till 2 November, when I collected all the eggs. The nest was apparently parasitized by at least 2 female cowbirds.

Nest 15: 1 October 1973, found with 2 sparrow eggs; 2 October, 3 sparrow eggs: 3 October, 3 sparrow eggs plus 1 immaculate cowbird egg; 5 October, 1 sparrow egg apparently punctured, otherwise no changes; 6, 8, 10 October, no changes; 12 October, all eggs vanished.

Nest 27: 24 September 1975, 1 sparrow egg; 26 September, 2 sparrow eggs plus 1 immaculate cowbird egg stained with yolk; 28 September, all eggs gone.

Nest 31: (the highest nest I found in the creeper Doxantha) 11 November 1975, 2 sparrow eggs: 12 November, 3 sparrow eggs; 14 November, no changes: 16 November, 3 sparrow eggs plus 1 spotted cowbird egg: 24–25 November, all sparrow eggs hatched; 28 November, cowbird egg hatched but nestling died.

Nest 36: Found on 23 November 1975 without eggs: 24 November, no eggs: 25 November, 1 immaculate cowbird egg: 26 November, 1 sparrow egg plus the cowbird egg: 27 November, 2 sparrow eggs plus the cowbird egg: 28 November, 1 sparrow egg (number 3, as both 1 and 2 removed) plus 2 cowbird eggs (1 immaculate, 1 spotted); 29 November, 1 sparrow egg (the same) plus 3 cowbird eggs (1 immaculate, 2 spotted) but nest
deserted. This nest retained all its contents till 3 December, then only the cowbird eggs till at least 18 December. The nest was probably parasitized by 2 female cowbirds.

The time of laying of the 11 cowbird eggs was as follows: 1 egg apparently laid before the egg-laying of the sparrows; 7 eggs laid during the egg-laying period; 2 eggs laid on the first day of the incubation period, and 1 egg laid on the fourth day of the incubation period. Sparrow eggs were removed either on the day when a cowbird egg was laid or on the previous or following day.

**CONTENTS OF PARASITIZED NESTS**

The 29 parasitized nests contained 59 cowbird eggs (average 2.03 eggs per nest) and 71 sparrow eggs which were eventually reduced to 62 (average 2.14 eggs per nest). The average number of cowbird eggs per parasitized nest in my sample was similar to the average of 2.06 cowbird eggs reported by King (1973: Table 1) from Tucuman.

As the mean clutch size in non-parasitized nests of sparrows was 3.18 eggs, this means that cowbirds removed an average of 1.04 sparrow eggs per parasitized nest, apparently a higher number than at Horco Molle or Rio de Janeiro (King, 1973: Table 1). I estimate that 30 eggs of sparrows were removed by cowbirds in my sample. I actually observed the disappearance of 9 sparrow eggs from 7 nests. In addition no fewer than 6 sparrow eggs were punctured but not removed.

I have no definitive records of cowbird eggs removed either by cowbirds or by sparrows. However I have observed 2 punctured cowbird eggs in 2 nests with 4 cowbird eggs each: both nests were abandoned on my next visit.

In my sample 15 parasitized nests (51.7%) contained 1 cowbird egg and 2-4 sparrow eggs (average 2.73 eggs); 4 nests (13.8%) contained 2 cowbird eggs and 2-3 sparrow eggs (average 2.75 eggs); 6 nests (20.7%) contained 3 cowbird eggs and 0-1 sparrow eggs (average 0.66 eggs); 2 nests (6.9%) contained 4 cowbird eggs and 2 sparrow eggs, and 2 nests (6.9%) contained 5 cowbird eggs and 0-2 sparrow eggs (average 1 egg). Thus the highest compound clutch was 7 eggs.

**Cowbird eggs.—**In my study area the eggs of Shiny Cowbirds are either immaculate or spotted (Fig. 1); this is normal in eastern Argentina, Uruguay, and southeastern Brazil (Friedmann 1929). Most immaculate eggs are white; the ground color of the spotted eggs as well as the number, size, distribution, and color of the spots shows a considerable and probably continuous variation. Intermediates to these basic types rarely occur. A few immaculate eggs may have some extremely faded pale gray spots resembling water marks on a white paper. These eggs were considered immaculate. In
the nests of Rufous-collared Sparrows, only 1 cowbird egg was considered to be intermediate, having a white ground color with 7 small deep brown spots. In my experience immaculate and spotted eggs are better regarded as discontinuous or quasi-discontinuous forms. This basic variation seems to be a true genetic polymorphism (Ford 1965). The possible selective forces that maintain this polymorphism are unknown. Immaculate eggs are strikingly different from the eggs of the local hosts of the Shiny Cowbird. Hudson (1920: 124–126) suggested that some host species may selectively reject or eject the immaculate eggs. At least 3 species among the recorded local hosts may eject cowbird eggs and at the present time I am investigating this point in the Chalk-browed Mockingbird. The Rufous-collared Sparrow is a poor subject for such studies, as it accepts eggs of both types.

Of the 59 eggs of Shiny Cowbirds found in nests of sparrows, 32 (54%) were immaculate, 26 (44%) were spotted, and 1 was intermediate. The
Fig. 2. Roundness (width × 100 length) of immaculate and spotted Shiny Cowbird eggs.

distribution of immaculate and spotted cowbird eggs in the parasitized nests was as follows: 10 nests received only immaculate cowbird eggs (7 with 1 egg, 3 with 2 eggs); 8 nests received only spotted cowbird eggs (7 with 1 egg, 1 with 3 eggs), and 10 nests were parasitized with both egg types in various combinations. One nest was parasitized with 1 intermediate egg. In the whole sample, 21 nests received immaculate eggs and 18 nests received spotted eggs. Available evidence suggests random placement of both egg types.

I measured 41 cowbird eggs (22 immaculate, 18 spotted and 1 intermediate). Average measurements (mean and standard error) are 22.75 ± 0.22 × 18.16 ± 0.18 mm for all the sample. Measurements of immaculate eggs are as follows: range: 20.7–24.3 × 16.8–19.8 mm; mean and standard error 22.56 ± 0.20 × 18.35 ± 0.19 mm. Measurements of spotted eggs are: range: 20.7–24.7 × 16.6–18.9 mm; mean and standard error: 22.91 ± 0.25 × 17.91 ± 0.17 mm. The intermediate egg measured 23.9 × 18.3 mm. As can be observed immaculate eggs are usually more rounded. The index for roundness (width × 100/length) ranges from 76.82 to 84.75 for immaculate eggs and 75.30 to 80.53 for spotted eggs. These values are plotted in Figure 2. The difference in roundness between the immaculate and the spotted eggs found in nests of sparrows is significant (P < 0.001, Mann-Whitney U-test and Kolmogorov-Smirnov test).

On the whole spotted eggs of Shiny Cowbirds do not closely resemble those of their hosts. However the spotted eggs are so variable that I have found a few exceptions in the nests of 4 host species. The smallest spotted cowbird egg
in my sample resembled the eggs of sparrows not only in size (20.7 × 16.6 mm) but also in color and pattern.

**Incubation period.**—In 2 parasitized nests of sparrows, 2 eggs of Shiny Cowbirds hatched in 12 days. Six eggs in nests of other hosts hatched in 11½ (1 egg) and 12 days. Four fresh eggs of cowbirds (2 from deserted nests of sparrows) placed in nests of Eared Doves (*Zenaida auriculata*) hatched in 12 days.

**Desertion of Parasitized Nests**

I did not observe Rufous-collared Sparrows to remove cowbird eggs of any type nor to practice egg-burial, but they may desert parasitized nests. The only possible case of desertion of a non-parasitized nest was attributed to predation. One sparrow egg was gone on the day of the desertion: the following day the destroyed nest cup was empty. I agree with Rothstein (1975) that nest desertion is not necessarily a direct specific response to cowbird eggs. The parasitized nests were perhaps deserted because the female cowbird was discovered by the sparrows, or because of the abnormal size of the clutch, or because some punctured eggs became glued to the nest lining.

As nests of Rufous-collared Sparrows suffer a high rate of predation, it is convenient to have a restricted definition of desertion. In this study I considered that 7 out of 29 parasitized nests were deserted due to cowbirds because: (a) eggs of host and parasite, or of both species, remained in the deserted nest, (b) the remaining eggs were not warmed and no sparrow was seen in or near the nest, (c) the nests retained their final contents for at least 1 day after their abandonment, or (d) I have evidence that cowbirds visited these nests either on the day of their desertion or (in 1 instance) on the previous day because new cowbird eggs were found or sparrow eggs were removed or punctured. The 7 deserted nests contained 20 cowbird eggs (11 immaculate, 9 spotted; average 2.85 eggs) and 13 sparrow eggs (average 1.85 eggs) and included the 2 nests with 4 cowbird eggs and one nest with 5 cowbird eggs.

**Interactions in the Nestling Period**

Due to the low nesting success only a limited number of eggs produced fledglings. In this section data from the additional 5 nests found in the nestling period are also included.

**Cowbird nestlings.**—Nestling Shiny Cowbirds from the nests of 6 host species showed variation in the color of the oral flanges and mouth lining, and in fewer cases in the color of the skin. The color of the flanges varied from pure white to yellow. The color of the mouth lining varied from pale
pink to deep red or orange-red. In at least 3 nestlings (1 from a nest of sparrows) the hue of the skin was yellowish.

These seemingly continuous variations were not obviously correlated with egg shell color. I have not detected correlation between the colors of the flanges and mouth lining. The fledgling cowbirds which were successfully reared by sparrows could be better described by comparison with the nestling sparrows, which have pale yellow flanges and red mouths. In 2 fledglings the flanges were white; 1 had a pale red mouth. The other fledglings had flanges which were at least as yellow as those of the sparrows; their mouth linings were red. The colors of the mouthparts were apparently irrelevant to the parental behavior of the sparrows. My largest sample of nestling Shiny Cowbirds comes from parasitized nests of mockingbirds, in which they often die of starvation; despite this, I have no conclusive evidence relating mouth color to survival value.

By day 3 cowbird nestlings have partially open eyes: by day 7–8 pin-feathers begin to emerge. Nestling cowbirds are less precocial in their behavior than nestling sparrows of the same age and do not attempt to leave the nest until day 11 or 12. The recorded nestling period of Shiny Cowbirds in nests of sparrows was 12–13 days but probably not all the nestlings departed spontaneously. In the safer nests of other hosts, the recorded nestling period was 13–15 days. Nestling Shiny Cowbirds seem to be less well adapted to the hazards of ground nesting than are nestling sparrows.

Table 2 gives the weights of nestling cowbirds and sparrows. King (1973) observed that the weight of a nestling cowbird is approximately equivalent to the weight of 2 nestling sparrows of the same age. In my study area I observed a similar situation. I found a pair of sparrows that fledged 4 young sparrows (in a nest found with nestlings), thus one might expect that 2 cowbirds could also be fledged at times. However in 3 nests in which more than 1 cowbird egg hatched only 1 nestling cowbird survived. Events in these nests were as follows:

**Nest 21**: found 27 October 1974 with 3 cowbird eggs (2 immaculate, 2 spotted) and 1 sparrow egg; 30 October, the spotted cowbird egg hatched: 31 October. the 2 immaculate cowbird eggs hatched (weights of nestlings—5.4, 3.4, 3.0 g): 1 November (weights 6.9, 4.4, and 3.7 g): 2 November (13, 6.8 and 5.8 g); 3 November, the 2 smaller nestlings were gone (the survivor weighed 18 g): 4 November, the nest was destroyed, the nestling vanished.

**Nest 23**: found on 8 December 1974 with 3 sparrow eggs and 2 cowbird eggs (1 immaculate, 1 spotted): 18 December. 2 cowbird nestlings (4.0, 3.7 g): 19 December, 2 cowbird nestlings (6.3 and 6.4 g): 20 December, 2 cowbird nestlings (8 and 7.7 g) plus 1 sparrow nestling (1.8 g): 21 December, only 1 cowbird nestling was alive (10.5 g); the other was dead from
Table 2
Weights (g) of Nestling Sparrows and Cowbirds*

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<th>Day</th>
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<td>2.0</td>
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<td>(1.9-2.1, N = 4)</td>
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<td>5.3</td>
<td>5.1</td>
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</table>

(* Nestlings that died of starvation are excluded.  
** Mean with range and sample size in parentheses.

unknown causes. The nestling sparrow was gone. Only 1 cowbird was fledged.

Nest 28 B: found on 12 October 1975 with 2 nestling cowbirds (weights: 12.5, 6 g); 15 October (weights 20 and 13.5 g); 17 October (27 and 16 g); 18 October, only 1 nestling (29.5 g) which was fledged on 22 October.

In 2 parasitized nests, 2 nestling sparrows were raised with 1 nestling cowbird. One nestling sparrow died of starvation in each of these nests. Another fledged cowbird was raised alone (no sparrow egg hatched).

NESTING SUCCESS

Sparrow eggs in non-parasitized nests.—Of the 35 eggs, 26 were taken by predators. Only 9 eggs hatched in 3 nests. Of the 9 nestlings, 3 were taken by predators: 6 were fledged. Only 2 of 11 nests were successful (18.2%). 9 of 35 eggs hatched (25.7%), 6 of 9 nestlings fledged (66.7%), and 6 of 35 eggs produced young which fledged (17.1%).
Sparrow eggs in parasitized nests.—I estimate that 92 eggs were laid in 29 nests; 30 eggs were removed by cowbirds. Another 13 eggs were abandoned in deserted nests, 23 eggs were taken by predators. Only 13 eggs hatched in 5 nests. Of the 13 nestlings 3 died of starvation, 4 were taken by predators, and only 7 were fledged. Only 3 of 29 nests were successful (10.3%), 13 of 92 eggs hatched (14.1%), 7 of 13 nestlings fledged (53.8%), and 7 of 92 eggs produced young which fledged (7.6%).

Sparrow eggs in all nests.—I estimate that only 13 sparrows fledged from 127 eggs laid (10.2%) in 40 nests.

Cowbird eggs.—Of the 50 eggs, 20 were abandoned in deserted nests. Another 27 eggs were taken by predators. Only 10 eggs hatched. Of the 10 nestlings, 3 died of starvation, 1 died from an unknown cause, and 2 were taken by predators. Only 4 cowbirds were fledged. Four of 29 nests were successful (13.8%). Of 59 cowbird eggs laid, only 10 hatched (16.7%), and of these nestlings, only 4 fledged (40%).

The figures for nest success are considerably lower than those reported from Tucuman and Rio de Janeiro (King 1973, Table 1). They are also the lowest figures for nesting success I have observed in local birds, but I have not studied other ground nesters. As most nests of sparrows in my sample were not found before egg-laying, the true nesting success could be even lower. My figures suggest that Shiny Cowbirds probably surpass any nest predator in the amount of harm inflicted to the reproductive efforts of the sparrows.

In my study areas nests built above the ground in trees and shrubs are exposed chiefly to avian predators and to the only abundant climbing mammal, the white-eared opossum (Didelphis albiventris). Nests built on or near the ground are probably equally exposed to opossums and to the most abundant avian predators (such as the Chimango, Milvago chimango) but in addition they are also exposed to other terrestrial predators, ranging from amphibians (the escuerzo, Ceratophrys ornata) to foxes (Dusicyon gymnocercus). Some terrestrial predators frequently seen in my study areas were hog-nosed skunks (Conepatus chinga) and great tegu lizards (Tupinambis teguixin).

The value of the sparrows as hosts of the cowbirds is considerably diminished by their high nesting losses. More extensive comparisons with other host species will be included in future accounts.

SUMMARY

Brood parasitism of Shiny Cowbirds on Rufous-collared Sparrows was studied in 1970-1975 in north Buenos Aires province, Argentina. Summary information on the local hosts of Shiny Cowbirds is reported. The overlap in the breeding seasons of cowbirds and sparrows was at least 87%. Shiny Cowbirds parasitized 72.5% of the nests. Non-parasitized nests were found almost throughout the breeding season of the
sparrows. Observations on the nest-searching behavior of female cowbirds are included. The sequence of egg-laying in 5 parasitized nests is described.

Parasitized nests contained an average of 2.03 cowbird eggs and 2.14 sparrow eggs. Cowbirds removed about 1 sparrow egg per parasitized nest. More than 50% of the nests were parasitized with 1 cowbird egg. Up to 5 cowbird eggs were found in parasitized nests. Cowbird eggs in nests of sparrows were immaculate (about 55%) or spotted (about 45%). Immaculate eggs are more rounded. Rufous-collared Sparrows deserted some parasitized nests.

The sparrows have a low nesting success probably because they are ground nesters. Few nests produced fledglings. Data on weights of nestlings suggest that sparrows cannot rear more than 4 nestling sparrows or 2 nestling cowbirds, but the latter situation was not observed.

SUMARIO

El parasitismo de cría de Molothrus bonariensis sobre Zonotrichia capensis fue estudiado durante 1970-1975 en una zona de estudio en Buenos Aires, Argentina. La superposición de períodos de postura fue de 87% y el porcentaje de nidos parasitados 72.5%. El promedio de huevos hallados en dichos nidos fue 2.03 para el parasito y 2.14 para el huésped. Los huevos del parasito eran inmaculados o manchados, con diferencias en la forma. Pese al bajo éxito reproductivo los datos sugieren que Zonotrichia puede criar hasta 4 pichones propios o 2 del parasito, aunque lo último no fué observado.

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LITERATURE CITED


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GENERAL NOTES

Sexual similarity of Red-headed Woodpeckers and possible explanations based on fall territorial behavior.—As discussed by Goodwin (Bull. Br. Mus. Zool. 17:1-44, 1968) the sexes are alike or nearly so in only 5 species of woodpeckers. In none of these are the sexes more exactly alike than in Red-headed Woodpeckers (Melanerpes erythrocephalus). This presents a challenging problem that has received little attention.

As narrated elsewhere, (Kilham, Wilson Bull. 70:347-358, 1959) 12 Red-headed Woodpeckers settled in one small wood of 1.7 ha in Maryland attracted by pin oak (Quercus palustris) acorns. The wood was divided into 12 sharply defined territories, each woodpecker defending its stores, chiefly against interspecific intruders.

In such situations, I suggest that the monomorphism of Red-headed Woodpeckers aids females in establishing and maintaining individual winter territories. If males dominated, the females would be crowded into less favorable habitats. This in turn might mean a poorer winter survival. If, however, as may have happened in their evolutionary past, females were selected to resemble males in plumage and hence have the same display colors, they would have a more equal chance in border contests.

The best parallel that I have been able to find for the sexual similarities in color of M. erythrocephalus is that described by Lack (Life of the Robin, H. F. and G. Witherby Ltd., London, 1943) for the British Robin (Erithacus rubecola). These birds form small, individual fall territories and the sexes have identical coloration.

One might ask how do juveniles before molting to adult plumage fare in competition with adults? As noted elsewhere (Kilham, op. cit.), among the 12 closely adjacent winter territories observed, the 3 held by juveniles were all peripheral and appeared to be the least desirable. The juveniles, therefore, without red heads, appeared to have fared less well, but lack of experience may also have been a factor.

It would appear from descriptions by Bock (Univ. of Calif. Publ. Zool. 92:1-100, 1970) that the Lewis Woodpecker (Asyndesmus lewis) resembles M. erythrocephalus in being irregularly migratory in relation to fall storage territories. This may account for the similarity in plumage between the sexes of this species. Acorn Woodpeckers (M. formicivorus), which are sexually dichromatic, also store mast in the fall. Living in social groups, however, and being to a considerable extent resident on the same territories the year around (MacRoberts, Condor 72:196-204, 1970) they are not exposed to the same selection pressures as are A. lewis and M. erythrocephalus.

Among sapsuckers, as well presented by Howell (Condor 54:237-282, 1952; Auk 70:118-126, 1953), the eastern Yellow-bellied (Sphyrapicus v. varius) is dichromatic and highly migratory whereas the western race, S. v. ruber, is monochromatic and essentially non-migratory. Are there any parallels to the situation encountered in M. erythrocephalus? In the absence of information as to whether S. v. ruber maintains fall and winter territories, I find it difficult to draw conclusions. It seems likely that monochromatism in birds can arise from more than one kind of selection pressure and that which I have described for an acorn-storing species of woodpecker may not apply, necessarily, to other Picines with other habits.—Lawrence Kilham. Dept. of Microbiology, Dartmouth Medical School, Hanover, NH 03755. Accepted 5 Feb. 1977.


Notes on the courtship behavior of Brown-capped Rosy Finches.—Published observations on the life history of the Brown-capped Rosy Finch (Leucosticte australis)
are scantly, the most comprehensive being those of Bailey and Niedrach (Birds of Colorado, Denver Mus. Nat. Hist., Denver, 1965), and Packard (in Bent, U.S. Natl. Mus. Bull. 237, part 1, 1968). These authors point to the lack of data on early breeding season activities and the courtship behavior of this species. In order to help fill the hiatus in our knowledge of the biology of these interesting birds, I offer the following notes on their courtship behavior.

Courtship display.—On 11 July 1977 I was looking for rosy finches in the upper portion of Navajo Basin (3700 m elev.) in the San Miguel Range, Dolores County, southwestern Colorado. At 10:45 a female finch landed in the fellfield near me and began to forage. Less than a minute later a male finch landed on a rock near the female and began to court her. His body was held low, feathers fluffed, tail held high above the back, head and neck stretched slightly forward and level with the back, throat swollen as he emitted a continuous chirping and rapidly fluttered his wings at his sides. He displayed for about 2 min then hopped off the rock and walked across the tundra toward the female. He continued to display as he followed her. His wing-fluttering became more pronounced, and he held his wings partly unfolded and away from his sides so that they caught the wind, making him appear off balance. The female then moved closer to the male, whereupon he flew at her and chased her in a horizontal straight line 1 m above the ground for 100 m before they disappeared behind some boulders, terminating the observations.

On 21 July 1977, I encountered many rosy finches around the base (3500 m elev.) of a prominent buttress above Stillwater Reservoir on the northeast edge of the White River Flattops in the Flattops Wilderness Area, Garfield County, northwestern Colorado. At 10:10 a male began to display before a female in the basalt talus about 10 m below me. The appearance of the display was like that described above with one major addition; the male picked up several long pieces of dried grass in his beak and held the material as he chirped and fluttered his wings like a begging juvenile. This display lasted about 2 min before the female showed her disinterest in the male’s efforts by flying off.

On 22 July 1977, I visited Medicine Bow Peak in the Snowy Range, Albany County, southeastern Wyoming, and found Brown-capped Rosy Finches along the base of the south face (3300 m elev.). At 16:45 a male followed a female into the boulders and began to display while perched atop a 2 m diameter rock as the female foraged below him. Again, his physical appearance and actions were similar to those described above. He picked up a piece of dried grass as he moved among rocks in rapid pursuit of the female. He dropped the grass when he reached another boulder, ceasing to display about 5 sec later when the female moved rapidly to the far side of the boulder out of his vision. At 17:00 I saw another male follow a female into the boulders and begin to display, but he barely had opportunity to begin when she apparently eluded him. He ceased to display immediately and sat silently for several minutes atop the boulder with his feathers fluffed.

The courtship display of the Brown-capped Rosy Finch seems to be similar to that of the Black Rosy Finch (L. atrata). The description provided by French (Auk 76:159–180, 1959) varies from what I saw in the Brown-capped males only in the elevated position of the beak. I saw nothing suggesting a female display. No coition was seen, and the late dates of these observations coupled with the lack of response shown by the females (except in the first case) may indicate that these males were courting already-mated females making foraging trips for their young (I saw fledged juveniles being attended by their parents at the last 2 localities). The persistent nature of un-
mated male rosy finches is well documented (French, op. cit.; Johnson, Auk 82:190-205, 1965; Twining, Condor 40:246-247, 1938).

An analysis of the courtship display described above seems premature, therefore I wish only to suggest a possible origin of the display based on my first impression. Hinde (Ibis 97:706-743, 1955; 98:1-23, 1956) summarizes an analysis he made of the courtship behavior of several species of finches, in which he concludes the male courtship displays are modified forms of the head-forward threat posture. My impression of the display of the male rosy finches is its similarity to the juvenile begging response, particularly the fluffed feathers, wing fluttering, and constant chirping. Morris (Behaviour 9:75-113, 156) mentions that in Estrildine finches feather postures are used as social signals, and a fluffed body posture can eliminate normal individual distances maintained by conspecifics, thus allowing individuals to approach one another until touching, without fear of attack. It seems possible that the display used by a male rosy finch acts to neutralize the expected agonistic response of the female upon his approach, and may even invite her closer approach. Male aggressiveness during courtship attempts, which Hinde (op. cit.) documents in a variety of Fringillids, may be more readily apparent earlier in the season.

**Flight display.**—Packard (op. cit.) includes observations by R. J. Niedrach of a "conspicuous song flight" that occurs during the mating season. I have observed this "song flight" perhaps a dozen times. In undulating fashion the male Brown-capped Rosy Finch flies a large horizontal arc or circle traveling several hundred meters, chirping (described in my field notes as a guttural *churk*) as he flaps his wings. During the breeding season rosy finches are often scattered throughout a cirque or basin making it difficult to visually locate conspecifics for courtship. The "song flight" of rosy finches may have the same function as the advertising song of other species (see Tinbergen, Trans. Linn. Soc. N.Y. 5:1-94, 1939) in that it serves to attract or locate potential mates. Finches on the ground often respond vocally to others flying overhead or nearby.

The vocal flight display of Brown-capped Rosy Finches may have evolved due to other selective parameters of the alpine environment. Morton (Am. Nat. 108:17-34, 1975) presents an argument for the ecological selection of non-ground song displays used by many grassland and tundra birds based on the effects of wind turbulence and solar radiation on sound propagation from the ground. It seems possible that the acoustic properties of an alpine environment, subjected to similar wind and temperature effects as grasslands and tundra, may have a similar selectivity for aerial song displays in alpine nesting birds. It is interesting to note that Horned Larks (*Eremophila alpestris*) and Water Pipits (*Anthus spinolletta*), both of which nest in alpine areas where rosy finches are found, also have flight displays (Verbeek, Wilson Bull. 79:208-218, 1967; Verbeek, Auk 87:425-451, 1970).

My field studies were funded in part by a Margaret Morse Nice Award generously provided by the Wilson Ornithological Society. I thank Drs. John P. Hubbard and Phillip L. Wright, and the reviewers of this paper for their help and suggestions, and I especially thank my parents for their continued support.—**PAUL HENDRICKS, 305 East Maplewood Ave., Littleton, CO 80121. Accepted 21 Feb. 1978.**


Manage. Inst., Wash., D.C., 1965) reported Starlings destroyed 23.8 and 20.6% of Wood Duck nests in Illinois boxes in 1963 and 1964 respectively, and usurped a large number of other boxes before Wood Ducks could use them. A similar situation has been reported by Muney and Burbank in Tennessee (Proc. Southeastern Assoc. Game and Fish Commissioners 29:493-500, 1975).

We conducted a Wood Duck nesting study at 10 sites in eastern Massachusetts during 1967-1973. Boxes were checked every 7 to 10 days between 2 June and 4 July and Starling nests removed. Starlings are persistent nesters. If a nest with a partially completed clutch is destroyed, the hen is capable of reconstructing the nest within a day and will frequently complete and incubate her remaining clutch (Kessel, Am. Midl. Nat. 58:257-331, 1957). If an incubated clutch is destroyed, the hen will begin a new clutch in 6-9 days (Royall, Condor 68:196-205, 1966). Consequently, we removed many more nests than there were pairs of Starlings present. Since individual Starlings were not marked, we did not know how many pairs may have used a given box. Observations on the stage of nest and clutch completion from 1 week to the next indicated that more than 1 pair of Starlings used some boxes. Once incubating Starlings were captured in a box and bird and clutch destroyed each week for 3 consecutive weeks. There was a 4th clutch the following week.

Figure 1 graphs the number of duck boxes used by Starlings and the total number of nests removed during the 1967-1973 period and for 3 years following when boxes were checked irregularly. It also shows the number of boxes used by Wood Ducks and Hooded Mergansers (Lophodytes cucullatus) during the same time span.

Starlings used 47 boxes on 7 sites in 1967 and 146 nests were removed. Nesting stages varied from nearly completed nests to completed clutches being incubated. Eight sites had Starling nests in 1968 and all 10 sites were used in 1969. The first results of the Starling nest removal program were noted in 1970 on a pond in Holden, Massachusetts. Starlings used 3 boxes on the pond in 1967, 2 in 1968, 1 in 1969 and did not nest in any box thereafter. Starlings nested on 6 sites in 1971, 4 in 1972, and in 1973 only 3 sites had Starlings; 21 nests were removed from 10 boxes in 1973.

During 1974-1976, Starling nests were removed when encountered, but checks were infrequent. As a result, a few broods were successfully fledged. Nests were started on 6 areas in 1974 and on 7 in 1975, but only 4 of these areas were used both years. The same 4 areas were the only ones used by Starlings in 1976. The minor increase in nests removed in 1975 (Fig. 1) is due to 1 site where boxes were checked every 3 to 4 days during May. As a result, 22 partially completed nests were removed from this area alone.

Kessel (op. cit.) states that Starlings suffer a 50% annual mortality and that the turnover period for a cohort to shrink to an insignificant portion of the population is 6 years. Assuming that the actual Starling population fell somewhere between the number of boxes used and nests thrown out (Fig. 1), it is apparent that the major portion of the Starling population was eliminated after 4 years of nest removal. Since reproduction from boxes was prevented during the 1967-1973 period, an influx of birds from surrounding areas was probably responsible for maintaining a small population.

Kessel (pers. comm.) indicated that in New York during the mid-1940s, there were always Starlings available from surrounding areas to take over vacated nest sites. We did not determine what the population levels were on areas surrounding our study sites, but current Massachusetts Breeding Bird Atlas data indicate the Starling is the second most common breeding bird in the state (R. Forster, pers. comm.). The fact that Starling production was eliminated on several of our study sites may have been due
Fig. 1. Number of Starling nests removed from Wood Duck boxes and number of boxes used by Wood Ducks and by Starlings.

to the areas holding isolated populations which, when removed, were not replaced. However, we cannot offer any definite reason for this occurrence.

The Starling control program did not increase waterfowl production. As many ducks used boxes in 1967 as in 1976 (Fig. 1). Duck production remained practically unchanged on 4 sites, increased on 3, and decreased on 3. However, many other factors
also affected production during this period including water drawdowns, nest predation, local hunting pressure, and vandalism. We believe that duck production would have decreased during the 10-year study period had we not removed Starling nests since Starling competition for boxes has been increasing since the early 1950s (Grice and Rogers, The Wood Duck in Massachusetts, Mass. Div. Fish. and Wildl., 1965).

Nest removal appears to be an effective but time-consuming method of controlling Starling populations in Wood Duck boxes. The use of Starling-deterrent nesting cylinders described by McGilvrey and Uhler (J. Wildl. Manage. 35(4):793-797, 1971) was evaluated by Heusmann et al. (Wildl. Soc. Bull. 5:14-18, 1977) previously. Grabill's (Wildl. Soc. Bull. 5:69-70, 1977) use of Starling boxes attached to Wood Duck boxes offers a third possibility for reducing competition for nesting sites between these species.

This study was a contribution of Massachusetts Federal Aid in Wildlife Restoration Project W-42-R.—H W Heusmann and Robert Bellville, Massachusetts Division of Fisheries and Wildlife, Westboro 01581. Accepted 31 Oct. 1977.


Unusual incubation behavior in Bobwhite.—A Bobwhite (Colinus virginianus) nest with an incubating hen was found on 26 September 1975, 8 km west of Starkville, Mississippi. The Bobwhite begins nesting in May in this area and this nesting effort was perhaps the pair’s 4th attempt. The nest and incubating hen were visited daily. On 3 October, when I attempted to photograph the hen on the nest, she left the nest giving the broken-wing ruse. The hen ran about 35 m from the nest and was joined by a male Bobwhite. The pair then flew off.

The nest contained 10 eggs, 1 of which proved to be infertile. One egg had successfully

![Fig. 1. Partially hatched Bobwhite eggs with dead chicks.](image-url)
hatched, but the chick was not found. The remaining 8 eggs contained fully developed but dead chicks. The chicks had pipped and partially ringed their egg shells and then became "entombed" (Fig. 1). Bobwhite chicks sometimes pip their egg shells but do not hatch due to weakness and/or desiccation (Stoddard, The Bobwhite Quail, C. Scribner's Sons, NY, 1931; Rosene, The Bobwhite Quail, Rutgers Univ. Press, New Brunswick, NJ, 1969; Stanford, Whirring Wings, Missouri Conservation Comm., Jefferson City, MO, 1952).

Stoddard (op. cit.) also said that Bobwhite have a strong nesting instinct and that an incubating hen may remain for a long period of time on eggs that do not hatch. The nesting behavior reported herein is interesting because the hen remained on partially hatched, dead chicks. Perhaps the stimulus of partially opened eggs kept the hen incubating. Also, it has been thought that if only one egg hatches, the nesting instinct would be satisfied (Murray and Frye, The Bobwhite Quail and its Management in Florida, Game Publ. No. 2, Florida Game and Fish Comm., Tallahassee, 1964). The 8 dead chicks had not started to decompose, but rather appeared to be desiccating. The length of time the hen remained on the partially hatched eggs is unknown, but the hatching effort probably occurred several days prior to 3 October.—GEORGE A. HURST, Dept. of Wildlife & Fisheries, Mississippi State Univ., Mississippi State 38762. Accepted 29 Dec, 1977.


A Cattle Egret-deer mutualism.—Cattle Egret (Bubulcus ibis)-ungulate relationships have been considered commensal (Heatwole, Anim. Behav. 13:79-83, 1965; Jenni, Ecol. Monogr. 39:245-270, 1969). Cattle Egrets feed more efficiently when taking insects flushed by grazing cattle than when hunting apart from cows (Dinsmore, Am. Midl. Nat. 89:242-246, 1973). We observed Cattle Egrets feeding on 3 species of horse flies (Diptera: Tabanidae) on the skin of the Virginia white-tailed deer (Odocoileus virginianus) in the Okefenokee Swamp, Stephen Foster State Park, 30 km NE of Fargo, Georgia from 28 May to 2 June 1977. This is the first reported association between Cattle Egrets and any North American nondomestic ungulate.

Observations (ca. 2.5 h) of several egrets and deer were made between 08:30 and 16:30 during the week. Commonly, 1 egret rode on the head or back of a deer and captured the large horse flies feeding on open wounds about the shoulder, head and face of the deer. The deer appeared undisturbed by the presence or feeding activities of the egrets. The species of horse flies observed (Tabanus petiolaris, Tabanus americanus, Diachlorus ferrugatus) inflict blood-letting wounds and may vector a variety of ungulate microbial diseases occurring in the southeastern United States (James and Harwood, Medical Entomology, Macmillan Publ. Co., New York, 1969). Thus because both egret and deer received benefits, the relationship was mutualistic. Whether the benefits are significant to the success of the individuals is unknown.

We thank Drs. Roland R. Roth and Richard W. Rust for comments on the manuscript. —MARC R. HALLEY AND WAYNE D. LORD, Dept. of Entomology and Applied Ecology, Univ. of Delaware, Newark, 1971. Accepted 3 Oct, 1977.


A test of significance for Mayfield's method of calculating nest success.—Mayfield (Wilson Bull. 87:456-466, 1975) presented further suggestions to simplify his
previously published method (Mayfield, Wilson Bull. 73:255-261, 1961) for combining all available nest data for a species to yield a less biased estimate of nest success than might otherwise be obtained. In his more recent account he included a test of significance that could be used for assessing the difference between estimates of success or, as in his example, the difference between "mortality rates" at separate stages in the nesting cycle, viz., between nest losses during incubation and nestling periods.

However, in simplifying his general methodology, I fear he may lead readers astray with the test of significance that he proposes. Most statistical texts clearly state that for a chi-square test, the elements in the contingency table must represent the frequencies of discrete, mutually exclusive attributes. This is certainly not the case when "nest-days with losses" are compared with "nest-days without losses" as in Mayfield's Table 1. Nest-days are arbitrary units, not discrete events. And any arbitrary time-interval, providing it is not less than the actual time required for the predation or destruction of a nest, can never have a frequency greater than the actual number of nests lost. Time-intervals without losses are, however, a function of the total time the nest was active.

Mayfield was aware of this problem. After finding that the test yielded a non-significant result, he stated: "...the difference may still be real. A larger sample might increase the confidence level. Changing to a smaller unit [my italics]—say, nest-hours—might seem to hold out promise of a different result, since it multiplies the sample size without enlarging the losses. ..." This very suggestion is a clear violation of assumptions underlying the statistical test. Normally, subdivision of the data would increase the calculated significance of the test, because the data in each class should be in equivalent units, e.g., failures versus successes. The caution against using chi-square tests on percentage data, echoed by so many texts (e.g., see discussions in Goldstein, Biostatistics, Macmillan, New York, 1964:102; Snedecor and Cochran, Statistical Methods, 6th ed, Iowa State Univ. Press, Ames, 1967:21; Vann, Fundamentals of Biostatistics, Heath and Co., 1972:156; Woolf, Principles of Biometry, Van Nostrand, Princeton, N.J., 1968:235), is a warning against an analogous procedure. If the total size of a sample were less than 100, then the use of percentages would artificially inflate the values in the contingency table and the analysis would indicate too great a significance. On the other hand, if the sample were greater than 100, the use of percentages would decrease the indicated probability that the difference is significant. Vann (op. cit.:164) indicates that to double the sample size in each cell of a contingency table is to double the chi-square value that will be calculated from it.

By suggesting, as does Mayfield, that "nest-days without losses" be increased by changing to hours [why not minutes? seconds?], while "nest-days with losses" cannot be changed because they are clearly fixed by nest losses, is to reduce the sensitivity of the test. As the denominator of each proportion is increased in this arbitrary manner, the proportions will both tend toward zero. It can be shown that when the sample size in only one column of a contingency table is increased, the calculated value of chi-square will increase; but, because the proportions are changing, as the sample size becomes infinitely large, chi-square approaches a finite value. This is quite unlike the situation when the sample size is increased in both columns of the contingency table, for then the proportions are unchanged and as the sample size becomes infinitely large, chi-square approaches infinity as it should. Thus the test proposed by Mayfield is too insensitive to differences between such proportions. In fact, the $\chi^2 = 1.16$ calculated by Mayfield cannot be increased beyond $\chi^2 = 1.20$, regardless of the increase in data to the column he suggests.

There seems to be no ready remedy. Although Mayfield's method might yield a less-
biased estimate of nest failure than obtained by ignoring nests other than those found before eggs had been laid, the fact remains that the only independent units available for statistical analysis are not nest-days or nest-hours but nests. The mortality rate that his method attempts to estimate is that which would be obtained if all nests could have been found and followed through the season, viz. failed nests/all nests. Thus, the only reasonable units for the marginal totals of the contingency table are the actual numbers of nests involved. I suggest calculating the frequencies within the table from the estimate obtained by Mayfield's method; this ensures the retaining of the accuracy of his method, while using only the total number of nests in the chi-square analysis ensures the satisfying of an important underlying assumption. This assumption is set unequivocally by Siegel (Nonparametric Statistics for the Behavioral Sciences, McGraw-Hill, New York, 1956:44): “To use \( \chi^2 \) in testing a hypothesis . . . cast each observation into one of \( k \) cells. The total number of such observations should be \( N \), the number of cases in your sample. That is, each observation must be independent of every other; thus one may not make several observations on the same person and count each as independent [read nest for person]. To do so produces an inflated \( 'N' \).” And on p. 109: “\( N \) is the sum of each group of marginal totals. It represents the total number of independent observations. Inflated \( N \)'s invalidate the test.”

The test I suggest is illustrated with Mayfield’s data in Table 1. Basically it can be seen to be an extension of Mayfield’s estimate of nest success itself. As he points out, to ignore incomplete records of nests is to bias results towards understating mortality and overstating success. He argues that his method brings mortality estimates to a more realistic level. My test makes use of these presumably more accurate estimates of mortality and survival to calculate the actual number of nests that should have failed or succeeded in a given sample of nests found at all stages. The data used by Mayfield in his Table 1 were based on 154 nests in the incubation period and 144 in the nestling period (Mayfield, The Kirtland’s Warbler, Cranbrook Inst. Sci., 1960:193, 198). From the estimate that he calculated, the actual number of nests lost in the incubation period must have been closer to 67.8 than the 35 that he observed. Likewise, losses during the nestling period must have been closer to 34.6 than to the 22 he noted. The chi-square test in Table 1 shows that the difference between mortality rate during incubation and

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<th>Table 1</th>
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<td><strong>Comparison of Mortality During Incubation and Nestling Periods of Kirtland’s Warbler (Dendroica kirtlandii)</strong></td>
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\( \chi^2 = 13.20; \text{ df } = 1; \ P < 0.0005 \)

* \( M = 1 - S \), where \( S \) is the average survival rate estimated by Mayfield (1975) for the incubation or nestling period; \( S = (1 - P)^n \) and \( P = 0.040 \) and 0.030, the mortality rate per nest-day; \( n = 14 \) and 9, the incubation and nestling periods in days.

† Calculated by multiplying ‘total nests found’ by ‘average mortality rate for period.’ Number of nests succeeded can then be obtained by subtraction.

‡ Obtained from Mayfield (1960).
nestling periods is in fact highly significant \((\chi^2 = 13.20; \ P < 0.0005)\), not non-significant as Mayfield concluded. Thus there would seem little justification for lumping the 2 stages to obtain a single rate. Mayfield stressed that the observer should state reasons for electing to lump or not to lump data from these 2 sources. The method that I have described provides an objective test of the homogeneity of the samples and thus a criterion to aid the decision to lump or not.

It may concern some readers that my test does not make use of “observed” and “expected” values as usually seen in a standard contingency table to be analysed by chi-square. They may prefer to think of the observations being made indirectly through Mayfield’s method; the marginal totals are in fact observed. However, it is important to realize that these values are established prior to and quite separately from the “expected” values in the standard chi-square analysis, and from the point of view of that analysis are indeed “observed” values.

Doubtless, more sophisticated analyses could be developed for data of this kind, but I think that chi-square still provides the easiest test and one that fits nicely with Mayfield’s desire to simplify the procedure as much as possible. As presented here, it has the advantage of being no more biased by sample size than Mayfield’s estimate of nest success might be, for the cell frequencies in the contingency table are based on that estimate. A possible source of bias, in some tests, lies in the fact that many nests from the nestling period are the same nests as those included in the incubation period, i.e., the rows of Table 1 may not be entirely independent. However, this will probably be of little importance and, in any case, will tend to make the test more conservative. Although not discussed by Mayfield, Yates’ correction for continuity (see any of the above references to statistical works) is sometimes applied to such \(2 \times 2\) contingency tables. But retention of the decimal part of the estimated numbers of nests will render this correction less important, although it will change the calculated chi-square value considerably if the sample size is small.

The method can be extended readily to tables with more than 2 rows and to other situations where tests of homogeneity are appropriate. The hypotheses under test, in any event, relate to differences between or among the estimates for incubation, nestling, or other periods obtained by Mayfield’s method.

Readers using Mayfield’s method should appreciate that the nest-day selected by him as the unit for analysis, although perhaps the most defensible on biological grounds because it provides a complete cycle for all possible predation, is an arbitrary choice. Mayfield does not discuss the selection of this unit, but his implication (1975 op. cit.) that nest-hours might be useful suggests that he is unaware of the difficulty. To change the unit of time also changes the success estimated for the overall period. For example, had his calculation of nest survival during incubation (from 35 nests lost in 878 nest-days of observation; daily mortality \(P = 0.040\)) been based on nest-minutes, he would have concluded that 57.23% rather than 56.58% of nests succeeded. At the other extreme, nest-fortnights (14 days is after all the incubation period of the species in his example) would yield a success rate of 44.19%. Other than through faith in the importance of circadian periodicity, it seems difficult to justify why the nest-day should yield the success rate closest to the actual one.

Although Mayfield devised his method ostensibly to reduce the bias of the conventional one, Green (Wilson Bull. 89:173–175, 1977) has shown that if a breeding population contains birds that can be categorized according to the vulnerability of their nests, Mayfield’s method will yield a biased result. Thus, when nests can be separated on any basis (e.g., habitat difference, age of owner, height, time in the season, first or
second clutch), it would appear advisable to use Green’s modification of Mayfield’s method. When such separation of data cannot be made, the dilemma of the researcher will be in not knowing whether the bias of Mayfield’s method towards understating success is greater or less than the bias of the conventional method in overstating it.—DOUGLAS D. DOW, Dept. of Zoology, Univ. of Queensland, Brisbane, Australia, 4067. Accepted 20 Jan. 1977.


**Mirror image versus conspecific stimulation in adult male Zebra Finches.—** Mirror image stimulation (M.I.S.) has been used to study social responses in a variety of animals (Kaufman and Hinde, Anim. Behav. 9:197–204, 1961; Svendsen and Armitage, Ecology 54:623–627, 1973). The advantage of this technique over direct visual contact with a conspecific is control of the stimulus by the experimenter. While this procedure has been conducted with several species, only chimps have so far shown the ability to recognize their own image (Gallup, Science 167:86–87, 1970).

Siamese fighting fish (*Betta splendens*) exhibit a preference for M.I.S. over visual access to a conspecific (Baenninger, Psychon. Sci. 4:241–242, 1966). This phenomenon also has been shown to exist in House Sparrows (*Passer domesticus*) and parakeets (*Melopsittacus undulatus*) (Gallup and Capper, Anim. Behav. 18:621–624, 1970). I examined this phenomenon in Zebra Finches (*Poephila guttata*).

Ten adult male Zebra Finches were tested in a continuous choice situation of M.I.S. and visual access to a conspecific. The testing apparatus was modified after the plan of Gallup and Capper (op. cit.). It consisted of a plywood box 72 cm long, 42 cm wide and 38 cm high. The ceiling had an opening 43 cm long and 26 cm wide covered by fine screen.

Two perches, 17 cm long, were placed 8 cm above the floor and centrally located on each side of the cage. One perch was associated with an 8 × 5 cm mirror; the opposite perch was placed in front of a plexiglass window of the same size. This window allowed visual access to a 14 cm long, 14 cm wide and 18 cm high target cage. The target cage contained one adult male conspecific. A cardboard partition in the test cage kept the test bird from seeing the stimulus associated with the opposite perch. A continuous supply of food and water was available in the target cage and on each side of the experimental cage.

Testing was initiated by placing one bird in the experimental cage and a conspecific in the target cage. A photoperiod of 12 h was controlled by a light source placed 40 cm above the testing apparatus. Time spent on each perch was electrically quantified. The weight of the bird on the perch triggered a microswitch hooked up to an electric timer. Timers were reset at the end of each 24 h period; this procedure was continued for a period of 9 days.

Figure 1 shows the amount of time spent on the perch associated with the mirror and the amount of time spent on the perch associated with the target cage. Day 1 was not included in the graph as this was considered an adjustment period. The data show an overwhelming preference for interaction with the conspecific compared to the almost total absence of time spent on the perch associated with the mirror. The preference for conspecific visual access continued until day 6 after which preference for M.I.S. took place. Preference for M.I.S. continued through the final 3 days of testing.

All of the 10 individuals tested showed an overwhelming initial preference for visual access to the conspecific and later exhibited a preference for M.I.S. which continued
Fig. 1. Mean time in minutes spent in front of a mirror (solid circles) and in front of a conspecific (open circles) by 10 adult male Zebra Finches as a function of time.

throughout the testing period. The earliest shift in preference took place on day 4 by 1 individual, and the latest shift was exhibited on day 8 by 2 individuals. One individual shifted preference on day 5, 2 on day 6 and 4 on day 7. Due to the abbreviated period of testing it was not possible to determine whether this shift was more than a temporary phenomenon.

The fact that after a period of time there is a definite preference for M.I.S. in adult male Zebra Finches suggests this phenomenon may occur among other bird species. The preference for M.I.S. was shown in the absence of auditory cues. This tends to support the hypothesis of Gallup and Capper (op. cit.) that the mirror image is being perceived as a supernormal stimulus. Superficially, there may seem to be little difference between the mirror image and the conspecific, but the mirror image will always be both predictable and compatible with the animal’s behavior. The mirror image may also be considered a novel stimulus. It has been demonstrated with guppies *Lebistes reticulata* (Russell, Anim. Behav. 15:586–594, 1967) that novel stimuli may be investigated less in a strange environment. This may explain the initial lack of interaction with the mirror image. The fact that the animal did not habituate to the image may be due to the abbreviated duration of the experiment. The complexity of a stimulus increases its novelty (Berlyne, Conflict, Arousal and Curiosity, McGraw-Hill, New York, 1960:43).
This may be true of the mirror image and at least partly responsible for the lack of habituation. Future work considering the preference for M.I.S. over an extended period of time with a variety of species may give some idea as to the adaptive significance of this behavior.

I would like to thank Roger J. Raimist for his helpful suggestions during study. Cindy Banas made the graph. This research was partially funded by the Student Research Committee, Life Science Dept., Glassboro State College.—Michael J. Ryan, Life Science Dept., Glassboro State College, Glassboro, NJ 08028. (Present Address: Dept. of Zoology, Rutgers Univ., Newark, NJ 07102). Accepted 30 Mar. 1977.


Protocalliphora infestation in Great Horned Owls.—On 5 May 1977, 6.4 km southwest of Foley, Minnesota, I collected several dipteran larvae from the ear cavities of a nestling Great Horned Owl, Bubo virginianus. I raised the larvae to adult flies, which were identified by Dr. Curtis W. Sabrosky, Systematic Entomology Laboratory, U.S. National Museum as Protocalliphora avium Shannon and Dobroscopy. The adult flies resemble blue-bottle flies, but belong to the family Calliphoridae; the blow flies. Protocalliphora have been found to parasitize a number of raptors, including Long-eared Owls, Asio otus (Shannon and Dobroscopy, J. Washington Acad. Sci. 14:247-253, 1924), and Red-tailed Hawks, Buteo jamaicensis. Red-shouldered Hawks, Buteo lineatus, and Cooper’s Hawks, Accipiter cooperii (Sargent, Auk 55:82-84, 1938). I found dipteran infestations to be quite common in Great Horned Owl and Red-tailed Hawk nestlings in central Minnesota. During the past 2 years, 41 of 73 (56%) Red-tailed Hawks, and 25 of 46 (54%) Great Horned Owls that I banded were infested. The larvae were located in the ear cavities of most nestlings although some were found in the nape area. Unfortunately, only from the one nest did I have the dipterans precisely identified. Other raptors may also be afflicted with this parasite, but there appear to be few documented cases. Protocalliphora eggs are apparently deposited in the nest debris; the larvae suck blood intermittently for 14-20 days and pupate for about 10 days before the adult flies emerge (Coutant, J. Parasitol. 1:135-150, 1915). The blood-sucking larvae usually do not seriously harm large species; however, they may weaken, kill, or force smaller passeriformes from their nests (Johnson, Ann. Entomol. Soc. Am. 22:131-135, 1929).—Robert T. Bohm, 520 7th Ave. North, Sauk Rapids, MN 56379. Accepted 21 Feb. 1978.


Territorial defense of a nectar source by a Palm Warbler.—Territorial defense of nectar has been documented in several species of wintering parulids, for example: Cape May Warbler, Dendroica tigrina (Kale, Auk 84:120-121, 1967; Emlen, Wilson Bull. 85:71-74, 1973), Palm Warbler, D. palmarum (Emlen, op. cit.), and Yellow-rumped Warbler, D. coronata (Woolfenden, Auk 79:713-714, 1962). It is the purpose of this note to document further the defense of a nectar source by a Palm Warbler and the disproportionate amount of time it spent chasing conspecifics from flowers as compared with the time spent chasing 2 other parulid species.

The following observations were made over a 5 h period (07:00-12:18) in Bayside Park, Miami, Florida on 9 March 1975. An unbanded Palm Warbler was observed
Table 1

Summary of the Time Spent in Pursuit by a Palm Warbler Defending Flowers of a Tiger's Claw Tree

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of pursuits</th>
<th>Average time of pursuit (sec)</th>
<th>Standard error</th>
<th>Range (sec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern Parula</td>
<td>24</td>
<td>39</td>
<td>1.4</td>
<td>25-61</td>
</tr>
<tr>
<td>Yellow-rumped Warbler</td>
<td>29</td>
<td>42</td>
<td>1.5</td>
<td>32-60</td>
</tr>
<tr>
<td>Palm Warbler</td>
<td>18</td>
<td>218</td>
<td>2.2</td>
<td>61-321</td>
</tr>
</tbody>
</table>

constantly as it defended the flowers of a Tiger's Claw Tree (Erythrina sp.). The leafless tree was 10-12 m tall with a crown diameter of approximately 10 m. The following species regularly visited the flowers on the tree but were not chased by the Palm Warbler: Common Flicker (Colaptes auratus), Red-hellied Woodpecker (Melanerpes carolinus), Fish Crow (Corvus ossifragus), Mockingbird (Mimus polyglottos), Starling (Sturnus vulgaris), and Spot-breasted Oriole (Icterus pectoralis). The Palm Warbler appeared to be actively defending the flower-covered tree from Northern Parulas (Parula americana), Yellow-rumped Warblers, and other Palm Warblers. Only parulids were chased from the tree. All chases were timed with a stop watch; only pursuits which I could see from start to finish are listed in Table 1.

The Palm Warbler seemed to be feeding on nectar during the observation period. For short periods of time (10-15 min) this individual stayed high in the tree calling and flicking its tail. From this location it often sighted and chased intruders.

From 09:00 to 09:30 this individual spent about 60% of the time sitting on a lookout perch, 30% chasing intruding parulids, and 10% feeding at flowers. This time budget is similar to that noted by Emlen (op. cit.) for a wintering Cape May Warbler defending a nectar source in the Bahamas.

My observations (Table 1) show that the Palm Warbler spent more time chasing conspecifics (average 218 sec per chase) from the tree than either species of parulid (average of 39 sec for parulas and 42 sec for Yellow-rumped Warblers). Comparisons of the average pursuit times for Palm with Northern Parulas and Palm with Yellow-rumped warblers both showed significant differences (p < .05) using a t-test. All 3 species fled from the territorial individual in the same manner and it is unlikely that the differences in pursuit times are due to differences in the behavior of the fleeing individuals.

Why more time and energy should be expended in the pursuit of conspecifics is not altogether clear. It is unlikely that a conspecific is more of a threat in nectar consumption than a parula or Yellow-rumped warbler. All 3 parulids appeared to feed in the same manner and presumably removed equal amounts of nectar. During 11 lengthy pursuits of conspecifics both Yellow-rumped and parula warblers flew into the unguarded tree and fed until chased by the returning territorial bird. The disproportionate amount of time spent in pursuit of conspecifics left the nectar source unguarded and thus available to other parulids. It appears that shorter pursuits of conspecifics would have been more efficient in guarding the tree from competing parulids.

The selective pressures for species recognition are probably quite strong and the appearance of a conspecific at a defended food source arouses a stronger aggressive
response than the appearance of other species. By responding more strongly to conspecifics, a territorial individual might leave the nectar source unguarded and thus available to other competitors. The rarity with which such nectar sources are encountered and the more unlikely condition that another larger species is not already defending it, give little time for selection to "finely-tune" this defense behavior. Nectar specialists, i.e., hummingbirds and sunbirds, tend to chase all competitors of the same size or smaller with equal vigor. The Palm Warbler which on rare occasions takes nectar might respond to a competitor with which it is most familiar. Aggression towards conspecifics is a common behavior found within the repertoire of possible responses and may account for the differential pursuit times.

Selection should favor defense of a feeding territory as long as the energy gained from exclusive use of that defended nectar source is greater than the energy expended in its defense (see Stiles and Wolf, Auk 87:467–491, 1970; Wolf, Condor 72:1–14, 1970). Generally interspecific dominance is based upon size, for larger species are either difficult or impossible to drive out of the territory. This territorial Palm Warbler ignored all intruding larger species and chased only parulid species of equal size.

I am grateful to K. W. Corbin, J. H. Rappole, P. J. Regal, and H. B. Tordoff for reviewing this manuscript.—Joseph M. Wunderle, Jr., Dept. of Ecology and Behavioral Biology, Bell Museum of Natural History, Univ. of Minnesota, Minneapolis 55455. Accepted 22 Feb. 1977.


Ring-billed Gull pair with 2 nests.—On 13 May 1975, I observed 2 nests of Larus delawarensis in the Calcite Colony (Rogers City, Presque Isle Co., Mich.) that were unusually close together. The nests had a common rim on one side and both contained eggs. Observations verified that only 2 gulls, apparently a pair, were attending the double nest. The nests were in a portion of the colony that has been used repeatedly since at least 1958.

The largest and most complete nest (i.e., that with the most nest material) contained 4 eggs while the other had 2 (Fig. 1). Two adult-plumaged gulls (i.e. lacked terminal tail bands and other characters normally indicative of birds less than 3-years old; see Ryder, Wilson Bull. 87:534, 1975) attended the nests. Each of the gulls consistently incubated the same clutch of eggs during my two 8-h observation periods before color-marking. Neither of the birds left the nest site while I was present on these 2 days. This represents unusually long incubation bouts for each bird as the mean duration of shifts for pair members at this colony is 1.8 h (Southern, pers. observ.).

The incubating birds were tolerant of one another and body contact was not unusual. Frequently the head of one bird touched the wing, tail, or back of the other. Occasionally their bodies were aligned parallel to one another facing in the same direction. The 2 gulls, either singly or in combination, threatened incubating neighbors and territory intruders. Both birds arranged nesting material, including that in the common wall between the nests.

Once the gull attending the 2-egg clutch left the nest and stood unchallenged near the adjoining nest. Before returning to the nest, it chased an intruding neighbor from the territory. While standing at the nest before settling, it again threatened the neighbor (with open-bill thrusts), this time in unison with its partner on the adjacent nest. During my observations no other gulls approached the double nest without being challenged by one or both attending gulls.
To determine if more than 2 Ring-bills were involved, the incubating birds were color-marked on the 3rd day of observation. This was accomplished by placing a paint-soaked swab of cloth on the nest rim so that any gull settling to incubate was marked on some part of its ventral plumage. Yellow was used at the 4-egg nest and blue at the other. Both gulls appeared somewhat alarmed by the presence of paint on the nest as they had resettled quickly following my previous daily check on nest contents. Following marking, the “yellow gull” rearranged nesting material as if attempting to cover up the spot. This action stimulated the other gull to contribute nest material and both worked on the spotted area. The gull attending the 2-egg clutch was hesitant to settle on the blue paint and after doing so immediately left the nest and stood nearby. Within 2 min it returned with nest material and worked on the painted area. About 10 min later both birds settled on their respective nests but the “blue gull” continued to rise and resettle. About 3.5 h later the blue gull ceased sitting on the nest and remained nearby with its plumage sleeked. It continued to defend the nest and eggs against intruders.

The following morning the yellow gull was standing near the 4-egg nest that now was being incubated by the blue gull. The 2-egg clutch had been abandoned and was not incubated thereafter. Four days later the 2 eggs were gone and the nest material, or at least that spotted by blue paint, had been incorporated into the remaining nest. The 2 gulls shared incubation duties thereafter at this nest. Four young eventually hatched and were cared for by both adults. Continuous observations were not made of the family group following hatching and so the role played by each adult in caring for the young is unknown.

Since the birds were not sexed it remains possible that the 2 gulls were other than a mated male and female (e.g. 2 females). Polygyny has been reported in other gulls (e.g. *Larus argentatus*, Shugart and Southern, in press) but in this particular case a 3rd
Clutch size and nest placement of the Pied-billed Grebe in Manitoba.—The Pied-billed Grebe (Podilymbus podiceps) breeds widely throughout North, Central, and South America (Palmer, Handbook of North American Birds, Vol. 1, Yale Univ., Press, New Haven, Conn., 1962). Despite this, relatively few studies of its breeding biology have been conducted. I obtained information at 2-4 day intervals between 19 May and 25 July 1973 on nest placement and clutch size of the Pied-billed Grebe in a prairie pothole area south of Minnedosa, Manitoba. This area has been described in detail by Ferguson (M.Sc. thesis, Univ. Manitoba, Winnipeg, 1977) and more generally by Ehrlich et al. (Man. Soil Surv. Rept. No. 6, 1957), Bird (Canada Dept. Agric., Contr. No. 27, 1961), and Keil et al. (Can. Wildl. Serv. Rept. Ser. No. 18, 1972).

Semi-drought conditions existed in the study area in 1973. The ephemeral and seasonal potholes (following Stewart and Kantrud, Resource Publ. 12, Bur. of Sport Fish. and Wildl., 1971) were dry or nearly so. The water levels in most semi-permanent and some permanent potholes were low, in some instances exposing entire stands of emergent vegetation.

In all cases (N = 53) only 1 pair of Pied-billed Grebes nested per pothole; this was also the case with most Horned Grebes (Podiceps auritus) nesting in the Minnedosa area (Ferguson 1977) and the Horned and Pied-billed grebes in North Dakota (Faaborg, Wilson Bull. 88:390-399, 1976).

Of 42 nests found with eggs in 1973, 29 failed; most of the failures were washed out before the clutches were completed. The average size of 22 completed first clutches was 6.8 eggs (1 of 5 eggs, 3 of 6, 17 of 7, 1 of 8). The mean size of 6 suspected replacement clutches was 7.2 eggs (5 of 7 eggs, 1 of 8). Glover (Wilson Bull. 65:32-39, 1953) also found no difference in size between first and first replacement clutches (see also Miller, Cassinia 32:22-34, 1943) and lumped them in his calculations. Palmer (1962) indicated that Pied-billed Grebe clutch sizes do not decrease as the season progresses. Ferguson (1977), however, noted such a decline in Horned Grebe clutch size in the Minnedosa area. The clutches used to calculate clutch size in my study were all initiated within a 2-week period from late May to early June.

I obtained additional information on Pied-billed Grebe clutch sizes in Manitoba, Saskatchewan, and Alberta from the Prairie Nest Records Scheme (PNRS) and for British Columbia from the British Columbia Nest Records Scheme (BCNRS). Nests where the clutch size was the same after 2 visits, 2-3 days apart, were used. The mean size of 6 such clutches from the PNRS was 6.7 eggs (extremes, 3 and 10). In 19 other nests visited only once by the observer, there were 5 with 6 eggs, 6 with 7, 5 with 8 and 3 with 9 (x = 7.3).

There is no apparent increase in clutch size from south-to-north in temperate North America (Table 1). The small clutches found in Idaho are not explained. The small sample of clutch sizes from Central America (Costa Rica, Honduras) suggests an overall latitudinal increase in clutch size. However, much more work needs to be done there on Pied-billed Grebes. In the Atitlan Grebe (P. gigas) of Guatemala, Labastile (Wildl. Monogr. No. 37, 1974) reported a mean clutch size of 2.9 eggs, with extremes of 2 and 5.
### Table 1

**Clutch Size of the Pied-Billed Grebe**

<table>
<thead>
<tr>
<th>Locality</th>
<th>No. Nests</th>
<th>Mean Clutch Size (Range)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Costa Rica</td>
<td>2</td>
<td>(3–4)*</td>
<td>F. G. Stiles (in litt.)</td>
</tr>
<tr>
<td>Honduras</td>
<td>1</td>
<td>5</td>
<td>Monroe (Ornithol. Monogr. No. 7, 1968)</td>
</tr>
<tr>
<td>Louisiana</td>
<td>67</td>
<td>7.0 (5–9)</td>
<td>Chabreck (Auk 80:447–452, 1963)</td>
</tr>
<tr>
<td>Pennsylvania</td>
<td>?</td>
<td>6 or 7 (5–9)</td>
<td>Miller (op. cit., 1943)</td>
</tr>
<tr>
<td>Iowa</td>
<td>97c</td>
<td>6.2 (2–10)</td>
<td>Glover (op. cit., 1953)</td>
</tr>
<tr>
<td></td>
<td>41d</td>
<td>4.3</td>
<td></td>
</tr>
<tr>
<td>Idaho</td>
<td>14</td>
<td>4.3</td>
<td>Wolf (J. Wildl. Manage. 19:13–23, 1955)</td>
</tr>
<tr>
<td>North Dakota</td>
<td>74</td>
<td>6.7 (4–11)</td>
<td>Stewart (Breeding Birds of North Dakota, Lund Press, Minneapolis, 1975)</td>
</tr>
<tr>
<td>Manitoba</td>
<td>22</td>
<td>6.8 (5–8)</td>
<td>This study</td>
</tr>
<tr>
<td>British Columbia</td>
<td>6</td>
<td>7.0 (5–9)</td>
<td>BCNRS</td>
</tr>
<tr>
<td>Alberta, Sask., Man.</td>
<td>6</td>
<td>6.7 (3–10)</td>
<td>PNRS</td>
</tr>
</tbody>
</table>

* It was not known whether the clutch of 3 was complete (F. G. Stiles, in litt.).

* In salt marshes.

* Successful clutches.

* Unsuccessful clutches.

Water depth measured at 31 Pied-billed Grebe nests averaged 35.5 cm. No nests were located in water less than 12.7 cm deep; 4 nests were in water 14–24 cm deep. A nest discovered on 28 June 1973, which contained 6 eggs (3 of them pipped), was in 14 cm of water, 0.3 m from shore. To leave the nest, the adult skittered on the water to open, deeper water 2.1 m away. The mean distance of 25 nests from shore was 5.3 ± 2.4 m and from open water, 1.3 ± 0.9 m. The dominant species of emergent cover at 53 nests was bulrush (*Scirpus* spp.; 37 nests, 69.8%), cattail (*Typha latifolia*; 15 nests, 28.3%), and white top (*Scholochloa festucacea*; 1 nest, 1.9%).

I thank R. W. Campbell and H. W. R. Copland for providing information on Pied-billed Grebe nests, contained in the BCNRS and PNRS, respectively. J. Faaborg and R. W. Storer commented on an earlier draft of the manuscript. A. Labastille, E. R. Blake, P. Slud, and F. G. Stiles kindly responded to my inquiry regarding clutch sizes of Pied-billed Grebes in Central America. Funds were provided by the National Research Council of Canada (A9556) and the University of Manitoba Research Board. This is contribution number 35 of the University of Manitoba Field Station (Delta Marsh).—Spencer G. Sealy, Dept. of Zool., Univ. of Manitoba, Winnipeg, Man. R3T 2N2. Accepted 10 Nov. 1977.
Nest placement in Sage Thrashers.—Nest site selection and placement has been shown to be important to nest success in various avian species (Goddard and Board, Wilson Bull. 79:283–289, 1967; Tenaza, Condor 73:81–92, 1971). Birds nesting in desert environments are particularly adapted to construct, place, and orient nests so as to maintain a favorable heat balance in eggs, young, and adults (Ricklefs and Hainsworth, Condor 71:32–37, 1969; Austin, Auk 93:245–262, 1976).

During the summer of 1976 I studied nest placement in Sage Thrashers (Oreoscoptes montanus) on the Snake River plain north of Pocatello, Idaho. The habitat is dominated by sagebrush (Artemisia tridentata). Of 15 first nests built and hatching young over the period 7 May to 29 May 1976, 13 were placed on the ground beneath the sage and close to the trunk. The average nest height was 2.9 cm from the bottom of the nest to the ground. Of 6 nests built and hatching young over the period 24 June to 14 July, 5 were placed off the ground in the branches of the sage. The average height of these nests was 22.7 cm. The difference in heights is significant, 0.005 < P(U > 79) < 0.01 (Mann-Whitney U test, Siegel, Nonparametric Statistics for the Behavioral Sciences, McGraw-Hill Book Co., Inc., New York, 1956). A typical nest is about 10 cm from top to bottom.

This difference in placement of first and second nests could be due to a number of factors. I do not know whether second nests were actually second broods of particular pairs or perhaps the nests of later nesting birds. The location of the later nests near first nests suggests the former. I believe the placement was a result of adjustment to avoid thermal stress. In May 1977 temperatures were recorded at the mean nest heights of 2.9 cm and 22.7 cm on 5 days, each day at a different location in the sagebrush. This mean maximum temperature at the upper position was 29.3°C and that at the lower 32.3°C. The mean minimum temperature at the upper position was –7.8°C and that at the lower –3.0°C.

Thus, first nests built early in the year and placed on the ground would benefit from the warmer temperature at ground level. Second nests placed higher in the sage and away from the main stem would benefit from air circulation and convective heat loss to the cooler air. This has been shown an effective means of heat dissipation from nests of the Cactus Wren (Campylorhynchus brunneicapillus) as reported by Ricklefs and Hainsworth (op. cit.).

Twelve of 15 first nests were built directly under a thick overhanging branch of sage, and another was placed under an old nest from some previous year. This would serve to reduce heat loss to the night sky as reported for hummingbirds (Calder, Condor 73:314–321, 1971). No second nests were built under thick overhanging structures.

The depth of nest cups, as measured after the fledging of young, was greater in second nests (8.2 cm) than in first nests (4.7 cm) though not significantly so, 0.10 < P(U > 17.5) < 0.20. I suggest that the deeper cups would protect the eggs and young from direct exposure to the sun while adults were off the nest.

No significant relationships were found with respect to orientation of nests from the main body of the sage.

This study was made while conducting research sponsored by the Frank M. Chapman Memorial Fund of the American Museum of Natural History and the Department of Biology, Idaho State University.—TERRELL D. G. RICH, Dept. of Biology, Idaho State Univ., Pocatello 83209. Accepted 28 Apr. 1977.
Great Black-backed Gulls breeding in salt marsh in New Jersey.—Great Black-backed Gulls (Larus marinus) have recently expanded in the northeastern U.S., nesting along the east coast as far south as Jamaica Bay, New York (Peakall, Kingbird 17:69–73, 1967), where they normally nest on sandy islands, shingles, moors, and grassy areas. In 1972, Parnell and Soots (Auk 92:154–157, 1975) found several adults and one nest on a dredge island in North Carolina. This report documents the invasion and successful nesting of Great Black-backed Gulls in the salt marshes of New Jersey. Since breeding behavior and success data are usually unavailable from the first pairs nesting in an area, I present these data.

In 1976, Great Black-backed Gulls nested on 5 salt marsh islands in Ocean County, New Jersey (39°41’–39°46’ N): 3 pairs on Clam Island, 2 pairs each on Sloop, Caravel, and Egg islands, and 1 pair on Sandy Island. Spartina patens and S. alterniflora dominate these low salt marsh islands with Iva frutescens growing in the higher areas. I checked nests on Clam Island 2 to 4 times a week from early April until late July, on Caravel Island weekly, and on the other islands once or twice a month.

On all islands Black-backed Gulls nested within Herring Gull (L. argentatus) colonies of 15 to 800 pairs. Laughing Gulls (L. atricilla) and Common Terns (Sterna hirundo) nested on Clam Island and Egg Island. Common Terns and Black Skimmers (Rynchops niger) nested on Caravel Island.

Black-backed Gulls generally nested under Iva bushes on grass in the center of the densest area of Herring Gulls. Channels divide Clam Island into several subislands, each containing one or more small areas with Iva bushes. On 9 April when I first visited Clam Island, I found 16 Herring Gull nest scrapes and 2 partially completed Black-backed Gull nests on the NE subisland, 10 Herring Gull nest scrapes and 2 completed Black-backed Gull nests on the NW subisland, and 8 Herring Gull scrapes and 2 Black-backed nests on the SE subisland. Although nesting activity began on all subislands at the same time, the Black-backed Gulls were separated by 500 to 800 m. Thus, Black-backed Gulls spaced themselves as if solitary with respect to conspecifics, but colonially with respect to Herring Gulls.

In all colonies Black-backed Gulls initiated egg-laying between 7 and 18 April, during the earliest period of egg laying for Herring Gulls. All nests found contained 3 eggs. Erwin (Wilson Bull. 83:152–158, 1971) found that Black-backed Gulls lay eggs earlier than Herring Gulls in Rhode Island and have a mean clutch size of 2.83.

Black-backed Gull eggs hatched first in all Herring Gull colonies. Hatching success on all islands was high (95%) compared to that reported by Harris (76%, Ibis 106: 432–456, 1964) and Erwin (44%, ibid). The high hatching success on Clam Island may be due to the lack of mammalian predators and the nesting synchrony in the area. Herring Gulls and Black-backed Gulls established territories at about the same time in these epicenters, thus eliminating behavior in defense of their nests which would have a disruptive effect. Erwin (ibid) attributed the low success to excessive territory defense on the part of the Black-backed Gulls because of their synchrony with the Herring Gulls. Within 10 days of hatching in New Jersey, the chicks entered the nearby channels and bays (5–20 m) when disturbed by humans. Generally the brood remained together with one or both parents flying overhead. Parents did not mob the intruder but left with the chicks. Chicks usually remained near land but sometimes swam 100 m away from the islands. After the intruder left, the parents flew back to the nest, landed, and gave repeated calls. The chicks, visually isolated from their parents and nest, returned to the nest within a half hour. Herring Gull chicks did not enter the water until consider-
ably older (over 25 days), and their parents mobbed human intruders. Perhaps one advantage of Black-backed Gulls nesting with Herring Gulls is the protection the attacking Herring Gulls provide.

Although Black-backed Gulls are well known predators on the eggs and young of other gulls and terns (Hatch, Auk 87:244–254, 1970), I did not observe any instance of Black-backed Gull predation on either eggs or chicks in over 560 h of observation from a hide where I could see 40 Herring Gull nests and 2 Black-backed Gull nests. Similarly I never found the remains of eggs or young near the 8 Black-backed nests regularly checked on Clam Island. Even though over 500 Herring Gulls were banded in the vicinity, Black-backed Gulls never regurgitated any bands near their nests. The mean clutch size of Herring Gulls was similar in areas with and without nesting Black-backed Gulls on Clam Island.

Black-backed Gull adults generally ignored the Herring Gulls nesting nearby, although the Herring Gulls appeared to move away from approaching Black-backed Gulls. Black-backed adults actively chased Herring Gulls only when Black-backed Gull eggs were hatching. When disturbed by a human, gulls circle overhead. During these disturbances, the Black-backed Gulls chased and pecked at any other gull flying over their nests and eggs.

Nine times I observed Herring Gulls initiate and successfully chase Black-backed Gulls when their chicks (as old as 32 days) approached adult Black-backed Gulls. I saw only 1 fight when a Herring Gull chick walked to within 1 m of a Black-backed nest and was chased by the resident adult. A fight ensued between the parents which involved pecking, wing flapping, wing tugging, and feather pulling. The Black-backed Gull subsequently flew and the Herring Gull chased its chick back the 5 m to its own nest.

Black-backed Gulls had high fledging success on the islands examined, as all pairs fledged 2 to 3 young (X = 2.42). Young were considered fledged once they reached 1300 g or were able to fly. Young from Clam and Caravel islands were weighed periodically and their weights were similar to those reported by Harris (ibid). It is difficult to obtain fledging rates for this species since they are often eliminated from mixed species breeding colonies by investigators interested in low predation rates (Harris, ibid). The high fledging rate in Ocean County, New Jersey may be the result of experienced breeders, high food supply, low predation rates, little conspecific competition for nest sites, or a combination of these factors. Mammalian predators are lacking from these low tide swept islands, and Herring Gulls do not yet appear to be as active predators on eggs as usual.

I would like to thank W. Vesterman for critically reading the manuscript and F. Lesser for valuable discussions and logistical support.—Joanna Burger, Dept. of Biology, Livingston College, Rutgers Univ., New Brunswick, NJ 08903.
PRESIDENT’S PAGE

(The following address was presented by Douglas James, President of the Wilson Ornithological Society, first at a recent conference on the amateur in ornithology held at the Cornell Laboratory of Ornithology, and later at the annual meeting of the Society this past May in West Virginia.)

Among the diverse facets of science and natural history, the study of birds has been particularly captivating to the lay person, the so-called amateur. Because of this rather unique and continuing interest, the science of ornithology has benefited through favorable public support. In return, the interested public has enjoyed the good feeling associated with becoming involved. The ornithologist seldom has fostered a schism of alienism that often pervades other scientific disciplines. Some would argue that this accessibility of ornithology to the general public actually has retarded progress in ornithology due to the inertia against changing concepts frequently encountered in the views of the non-scientist. This, of course, is a debatable point. A consideration that is not controversial, however, is the acknowledged large contribution lay members of ornithological societies make through dues payments in supporting the ornithological journals. Thereby the amateur greatly expands the opportunity for publishing the fruits of scientific labors produced by the practicing ornithologist. This has to count as an outstanding contribution of the amateur to the success of ornithology. Admittedly, this large lay audience may exert a subtle negative influence on the quality of the journal contents, but this factor certainly must be outweighed by the implemented great increase in number of journal pages. Because of this kind of amateur support, there are 5 ornithological journals in this country that receive national and international circulation. This is an enviable position not enjoyed by any of the sister sciences in vertebrate biology. On inspection of membership rolls of the societies supporting these ornithological journals, it is strikingly obvious that the proportion of amateurs as members is much higher than the proportion of amateurs that publish in the same journals. The professional ornithologist is overrepresented in the publications and thus benefits greatly from support from amateurs.

The Wilson Ornithological Society is one of these journal societies. An appraisal of its activities clearly indicates that its main focus pertains to maintaining a quality journal in ornithology, The Wilson Bulletin. The only coordinated group activity of the Society is the annual meeting, which is attended by merely 10% of the members. This is comparable to meeting attendance ratios of the other major ornithological societies. Therefore, the Wilson Ornithological Society, like the others, reaches its membership, stimulates their interest, and attracts their support primarily through the publication of a journal devoted to papers in original research in ornithology. I cannot emphasize enough the importance to ornithology of the amateur’s role and interest in supporting this enterprise.

Recognizing this present day situation, it is interesting to note that The Wilson Ornithological Society was indeed founded by amateurs, and by perhaps the most uninitiated cadre of amateurs, depending on one’s view. In fact, the charter members in 1888 were a group of pre-college boys. The details have been stated before, so I need not dwell on them here, except to say that many of these 36 youths previously had become acquainted in an organization called the Young Ornithologists’ Association. Most originally had met through correspondence in response to egg exchange advertisements in The Oologist, but they were interested in more than just data gathering, and lacking a
deep knowledge of anatomy, physiology, and taxonomy, they wanted to conduct meaningful studies in field ornithology. Even in those early years the membership had a coast to coast scattered distribution united only by a publication that eventually became The Wilson Bulletin.

All this emphasizes the early tradition of the amateur in ornithology in the Wilson Society. And I purposely say “the amateur in ornithology” which is vastly different from what would have been incorrectly implied by the phrase “amateur ornithologist.” Some of these lads eventually became professional biologists. George Hall, who has reviewed all the past issues of the Bulletin, informs me that this prevalence of the amateur characterized the Society until the time of World War II. After that, the proliferation of professional ornithologists was conspicuous and it continues to be a significant trend in the Society.

So far I have described how the Wilson Society was at first a wholly amateur enterprise, becoming transformed more recently into a noteworthy support of ornithology through amateur participation in Society membership. This latter, of course, is a passive relationship. The Wilson Ornithological Society also provides an active support of the role of the amateur in ornithology. I think more properly stated, it provides the amateur with the opportunity to become significantly involved in and make contributions to ornithology. The Society directly encourages ornithological research by amateurs through the annual Margaret Morse Nice Awards, which are grants in support of research given to deserving applicants who are not professional ornithologists. The annual Edwards Prizes for the most significant papers in The Wilson Bulletin reward amateurs when they happen to be the prize winning recipients. And, in fact, the Bulletin is an avenue for publication of research projects conducted by amateurs, whether members or not. Many amateurs have taken advantage of the open forums at annual meetings of the Society to present the results of their research on the program for scientific papers. Also, amateurs frequently are officers of the Society, and thereby play an especially significant role in ornithology. Finally, the Society offers a particularly important opportunity to amateurs, and all members, in maintaining the Van Tyne Library at the University of Michigan. Holdings in avian biology in this library collection are available on loan to any society member; this provides access to items that are not available in most local libraries used by amateurs.

Everything about the encouragement of amateurs by the Wilson Society, and the involvement of amateurs in the Society, speaks to a personal rather than a coordinated group participatory relationship. There are no programs comparable to the Christmas Bird Counts, Breeding Bird Survey, bird banding efforts, or nest record schemes, specifically originated and coordinated by the Society. I do not view this as a mindless deficiency on the part of the Society. The amateurs in the Society who have made really significant ornithological contributions have described to me how their inspiration derived from personal contact with scientists in the Society, made possible of course by the existence of the Society, but not arising from any special group program sponsored by the Society.

Therefore, Kenneth Parkes is correct in reminding me that the Wilson Society has been very instrumental in encouraging amateurs on an individual basis, but has not been especially concerned with developing group participation projects that mobilize amateur efforts focusing on specific ornithological problems. Nevertheless, elsewhere there certainly have been significant group efforts of this kind, more should be developed, and The Wilson Ornithological Society would be pleased to offer its facilities to assist in any way it can.
In view of the successful experience of the Wilson Society with regard to the participation of the amateur, I would make a recommendation concerning group projects in ornithology. I think that the reason the Wilson Society survived and flourished under the blend of amateur and professional expertise is that both groups realized a common goal of accomplishment. This means that amateurs like professionals were encouraged not only to gather pertinent data relative to their studies, but also could follow through in data analysis, and could develop the conclusions pertaining thereto. If more group projects are forthcoming that involve the mobilization of amateurs to collect ornithological data relating to important avian research problems, then the same amateurs, to really become involved and motivated, should have the opportunity in these projects to participate in the data analysis, data interpretation, and in forming appropriate conclusions. This to me is the real lesson arising from the past experience of The Wilson Ornithological Society and is the overriding dominant principle that spells success to the cooperation between the amateur and professional in producing significant advances in the science of ornithology.

ORNITHOLOGICAL NEWS

NOTICE TO CONTRIBUTORS

Effective immediately, new manuscripts to be considered for publication in the Wilson Bulletin should be sent to editor-elect, Dr. Jon Barlow, Department of Ornithology, Royal Ontario Museum, 100 Queen’s Park, Toronto, Ontario, Canada M5S 2C6. Correspondence concerning volume 90 of the Wilson Bulletin should be sent to the present editor.

HAWK MOUNTAIN RESEARCH AWARD

The winner of the first annual Hawk Mountain Research Award was James C. Bednarz of Iowa State University for his studies of the “Status and habitat utilization of the Red-shouldered Hawk in Iowa.”

The Board of Directors of Hawk Mountain Sanctuary Association announces its second annual award of $250 for support of raptor research. The Hawk Mountain Research Award is granted annually to a student engaged in research on raptors (Falconiformes).

To apply, students should submit a description of their research program, a curriculum vitae, and two letters of recommendation by 31 October 1978 to: Mr. Alex Nagy, Hawk Mountain Sanctuary Association, Route 2, Kempton, Pennsylvania 19529.

A final decision will be made by the Board of Directors in February 1979.

Only students enrolled in a degree granting institution are eligible. Both undergraduate and graduate students are invited to apply. Projects will be judged competitively on the basis of their potential contribution to improved understanding of raptor biology and their ultimate relevance to conservation of North American hawk populations.
MANAGEMENT OF NATIONAL WILDLIFE REFUGES IN THE UNITED STATES: ITS IMPACTS ON BIRDS

National Wildlife Refuges administered by the U.S. Fish and Wildlife Service, Department of Interior, occur in 49 of the 50 states and encompass more than 13,678,860 ha. While much of the present refuge system was acquired for management of migratory waterfowl, refuges have been acquired for preservation of “endangered” species ranging from Whooping Cranes (Grus americana) to the Dusky Seaside Sparrow (Ammodospiza nigrescens). Refuges have been acquired through withdrawal from the public domain, donations, outright purchase, leases, easements, and acceptance of lands administered by other agencies. Consequently due to the diversity of habitats and species, origin, location, etc., National Wildlife Refuges have different values to different interest groups. Despite having wildlife-oriented missions, some refuges have been managed for grazing, recreation such as boating, lumber products, commercial crops, etc. with frequent adverse effects on achieving desired wildlife objectives. Multiple and single uses of refuges contrary to initial objectives when refuges were acquired have resulted in internal and public criticism. These problems coupled with inadequate funding and staffing have led to outside review of the overall system (Leopold 1968). More recently intense dissatisfaction with the U.S. Fish and Wildlife Service’s (USFWS) “management by objectives” approach to budgeting (resulting in no program specifically for refuges, continued inadequate funding of the refuge system, and a host of other alleged problems) has led to much internal and public commentary on the desired future of the refuge system. These problems led to preparation of draft and final environmental statements concerning operation of the National Wildlife Refuge System (USFWS 1976b). During 1976 and early 1977 The Conservation Committee of The Wilson Ornithological Society solicited comments on and reviewed major practices on National Wildlife Refuges. The complexity of the refuge system, funding restraints, inherent operational problems, legislative authority, etc. were such as to overwhelm the Committee. Consequently it was decided to identify major practices on refuges affecting birds that could conceivably be altered to enhance avian habitats and populations. The report relies heavily on the waterfowl literature as data concerning raptors, colonial waterbirds, and other non-game birds on refuges were generally not available.

HISTORICAL PERSPECTIVE

President Theodore Roosevelt, by executive order on 14 March 1903, set aside Pelican Island as the first federal bird refuge. By the end of his first term in 1904, Roosevelt had created 51 wildlife refuges in 17 states and 3 territories. The Weeks-McLean Bill, attached as a rider to the Agricultural Appropriations Bill and signed unknowingly by outgoing President William Howard Taft, gave the federal government authority over migratory birds in March 1913. The intent of the Weeks-McLean Law, considered an unconstitutional invasion of state’s rights, was given added authority by the Migratory Bird Treaty between the United States and Great Britain (for Canada) in 1916. Then, in 1918 Congress passed and President Woodrow Wilson signed the Migratory Bird Treaty Act.

The various treaties and laws were regulatory and, although migratory species responded with increased numbers for a time, it became clear that long-range problems and solutions were in protection of habitat. Refuges established by executive order were too few and scattered to insure the future of migratory species. The first attempt to
launch a program came in 1921 with bills that would establish a refuge system, a Migratory Bird Refuge Commission, and a one-dollar federal hunting stamp. Labeled as a “duck slaughter” bill, it failed 4 times in Congress. Finally, in 1929, a bill passed, but only after stripping it of any shooting ground provisions and the federal hunting stamp. It was to be funded with Congressional appropriations.

Concern for migratory species, especially waterfowl, increased as their numbers declined with the drought of the 1930's. Congress failed to appropriate funds for the refuge system authorized in 1929. As a result of increasing concern, the federal hunting stamp proposal was revised and finally passed in 1934. With a source of revenue and the leadership of Jay “Ding” Darling, the National Wildlife Refuge System advanced from a few scattered units to the system of 367 refuges that we have today.

Legislative authority, executive orders, and international treaties have given the federal government responsibilities for all species occurring on refuges. These range from elk (Cervus canadensis) on the National Elk Refuge in Wyoming, to the endangered Whooping Crane on the Aransas National Wildlife Refuge (NWR) in Texas. But, for all these responsibilities, the refuge system’s major focus and objective has been the preservation and management of waterfowl. At the fiscal year 1974 level, 276 (75%) of all refuges were managed specifically for waterfowl production, migration, or wintering. Wildlife and Game Ranges and Big Game Refuges have principally been established by withdrawals from the public lands. Over 9.5 million hectares in 24 units are in this category. On 68 refuges, encompassing over 1.6 million hectares, management must be directed toward certain species of colonial nesting birds.

Maintenance of the National Wildlife Refuge System has not kept pace with the early interest shown in its establishment. During the system’s expansion more than 11,000 people were engaged in developing critical wildlife habitat. But, this support was not so much for the refuges and their wildlife, as it was for the Civilian Conservation Corps and the jobs it created during the Depression. Recently, USFWS Director L. A. Greenwalt testified, “The National Wildlife Refuge System, as with most activities of our Service, has been underfunded for some time. The consequences are evident in facilities which are inadequate and poorly maintained. Too few people are available to do a proper job of refuge management.” Much needed funding and personnel for the refuge system have been diverted to new responsibilities—energy research and development, wilderness studies, Youth Conservation Corps, endangered species, and marine mammals. These activities have not been funded on their own merit, but at the expense of the National Wildlife Refuge System. During the 1975 fiscal year, refuge field operations were funded at about $20 million, $7.1 million less than the 1970 funding level. The USFWS has estimated that, to fully develop the entire system to provide optimum wildlife and public benefits, $170 million would be needed. To maintain that level of operation, an additional $34 million and 2000 man-years of labor would be needed annually. The Carter administration has recommended a 30% increase in the level of funding for the USFWS. It proposes additional personnel ceilings under the Bicentennial Land Heritage Program.

MAJOR REFUGE MANAGEMENT ACTIVITIES THAT AFFECT BIRDS

Grazing

According to the Final Environmental Statement on the Operations of the National Wildlife Refuge System (USFWS 1976b), in Fiscal Year 1974 (1 July 1974–30 June 1975) 740 grazing permits were issued to private citizens for approximately 526,110 ha
of refuge land. These 740 permittees used 354,589 Animal Unit Months (AUM’s). Grazing occurred on 103 refuges in 36 states, using 4% of the total area on National Wildlife Refuges. Areas grazed in addition to rangeland included native wet meadows and riparian sites which are used extensively by nesting waterfowl and other birds.

The number of hectares grazed in each flyway were: Atlantic—5,947, Mississippi—10,360, Central—158,321, and the Pacific—331,887. In addition, about 6475 ha were grazed in Alaska. Forty-five percent of the 1,157,235 ha of rangeland in the system were used by cattle. Nearly 70% of the total grazed area occurred in 3 states: Montana (8 refuges), Nevada (5 refuges), and Oregon (4 refuges).

Although a logical assumption would be that the high grazing use in the Pacific Flyway mostly occurs on big game refuges, such as Hart Mountain NWR, Oregon, Sheldon NWR, Nevada, and National Bison Range, Montana, such is not the case. Malheur NWR, Oregon, a waterfowl and waterbird production area, had 98,502 AUM's in 1974-75, or 27.8% of the national refuge AUM total. Hart Mountain NWR had only 11,000 AUM's or 3.1% of the national total. Sheldon NWR, which is considered over-grazed, had 24,000 AUM's (6.8%) while the National Bison Range had no cattle grazing.

The present USFWS policy is that grazing and haying programs be used to manipulate vegetation to maintain or increase wildlife productivity and species diversity over a sustained period of years at minimal cost to the government, and that grassland habitat should be maintained for the primary benefit of wildlife populations. Grazing and haying activities may be permitted to enhance, support, and contribute to established wildlife management objectives, but must not conflict with those objectives (USFWS 1976b). Unfortunately, when grazing is allowed, the USFWS frequently loses control of local situations due to intense political pressure at all levels of administration.

At least 55 waterfowl studies have shown that grazing is detrimental to waterfowl production. Only one study reported higher success on moderately grazed areas than on idle areas (Burgess et al. 1965). Anderson (1957) reported that 42.2% of the 116 nests on idle land in California hatched, while none of 7 on grazed land hatched. Glover (1956) found 24.4% nesting success on idle land and lightly grazed areas in Iowa, compared with 10.5% success on moderately and heavily grazed areas. One study had nest losses of 80% in light cover, compared with 29% in dense cover (Schranck 1972). Weller et al. (1958) reported that the effect of cattle grazing on vegetation in Utah was as serious as the lack of water. On Malheur NWR, Oregon, Greater Sandhill Crane (Grus canadensis tabida) nesting success in 1976 was 54.6% in mowed-grazed, 63.6% in mowed-ungrazed, and 84.2% in unmowed-ungrazed areas (C. D. Littlefield, unpubl. data).

Grazing was reduced sharply in some regions of the United States after a memorandum was released 22 December 1972 from the Director. USFWS. It stated “Recent research at the Northern Prairie Wildlife Research Station at Jamestown, North Dakota, indicates that having and grazing are incompatible with upland nesting duck and ground nesting bird objectives. . . . While the recommendations apply primarily to the north central region of the United States and the southern Prairie Provinces of Canada, application of these practices on refuges in other geographic areas have demonstrated similar favorable response by waterfowl and other ground nesting birds.”

In North Dakota, AUM's were reduced after this memo, but by 1975 had increased, with additional increases planned in the future. At J. Clark Salyer NWR, North Dakota, three-quarters to 1 AUM per acre (.4 ha) was used in 1976 (total 2600 AUM's), but present plans are to increase the use to 2 AUM's per acre. Other examples in North Dakota include Arrowwood NWR with 435 AUM's in 1971; 1109 in 1975; and 1650
projected for 1979. Upper Souris NWR had 2348 AUM's in 1971; 2348 in 1975; and 5634 are projected for 1979.

The most serious grazing problems on National Wildlife Refuges appear to occur in Oregon and Nevada because of local political pressure with over- or untimely grazing being typical of most western refuges. Examples given are but a small sample of the problems associated with this management "tool."

In 1948 on Malheur NWR, waterfowl production was 150,000 ducks, but in 1974 only 21,300 were produced. In 1948 AUM's were 74,385, increasing to 101,726 by 1951. In 1961 and 1971 AUM's were 122,404 and 123,807 respectively. As AUM's increased duck production decreased. From 1962 to 1972 the average number of ducks produced annually was 29,600. Mallards (Anas platyrhynchos), which are dependent on residual vegetation from the previous year for nesting cover, declined from 50,000 produced in 1949 to 2,120 in 1974. Some changes in grazing practices are presently occurring at Malheur. By 1975-76 AUM's had been reduced to 88,221. After considerable pressure from environmental groups in 1976, AUM's were reduced to 65,828. In addition, 1712 ha were mowed for hay. By 1977, 8782 ha were in "non-use," compared with 263 ha in 1962. At Malheur NWR the grazing program requires over 338 km of internal fences. In 1976, to protect river banks and dikes from severe cattle trampling, several km of additional 3-wire fences were placed between heavily grazed areas and canal and river banks. These new fences have resulted in many Sandhill Crane (Grus canadensis) pairs having their traditional territories bisected with barbed wire. Obviously, grazing in this situation does not enhance refuge objectives but instead creates conflicts with adverse effects on bird populations.

Wildlife collisions with fences are common. Mule deer (Odocoileus hemionus), pronghorn (Antilocapra americana), and numerous birds have been killed flying into or becoming entangled in fences. Greater Sandhill Cranes have been killed at Malheur and Grays Lake NWR, Idaho. Flightless young Whooping Cranes became entangled in barbed wire fences on a number of occasions at Grays Lake NWR, in 1975. One young Whooping Crane died in 1976 near Monte Vista NWR, Colorado, after colliding with a fence. At Red Rock Lakes NWR, Montana, several moose (Alces alces) calves have died from injuries sustained after becoming entangled in fences. At times, simple modification of fences can be beneficial. While over 20 km of interior fences have been removed at Grays Lake NWR, virtually all of the remaining fences have been modified from 4-5 to 3 wires. This has greatly improved movements of young cranes. Of importance is the obvious fact that fences have little value for wildlife. They are expensive and are placed on refuges primarily to enhance livestock grazing.

On many refuges, power lines transect nesting areas or bisect principal flight paths. Some of these power lines bring electricity to pumps that supply water for cattle. Power lines are a major mortality factor for swans, cranes, eagles, and other large birds. At Bosque del Apache NWR, New Mexico, aircraft markers have been placed on lines and some lines have been buried. Mortality has been dramatically reduced. On other refuges either the pumps should be removed or power line markers should be placed at strategic locations in wildlife use areas. Preferably the lines should be removed or buried.

At Stillwater NWR, Nevada, the USFWS operates the refuge with a cooperative agreement between the Bureau of Reclamation, Nevada Fish and Game Department, and the Truckee-Carson Irrigation District. Much of the 90,653 ha refuge is unfenced and cattle move onto the area freely. On the portion that is fenced, grazing is permitted for 11 months annually; total refuge AUM's is 15,000. Refuge areas are leased from the Bureau of Reclamation by the local irrigation district. Refuge personnel collect AUM
fees, issue permits, and count livestock on and off the refuge. In return, all fees collected are given to the irrigation district. Most grazing is determined by the district and attempts to reduce AUM's have failed (one permittee is a member of the irrigation district board).

Napier (1974) in his recommendation for Stillwater Marsh, stated “Grazing was used as a tool for opening up shorelines overgrown with dense stands of cattail and bulrush in Stillwater Marsh's early history. The result was increased duck production. Now, poor water conditions have resulted in a downward trend or elimination of emergents on some impoundments. Management is now aimed at encouraging emergent aquatic growth. Livestock grazing in the marsh is detrimental in this respect, for cattle heavily graze the emergent vegetation.” Because the Bureau of Reclamation, a sister agency of the USFWS in the Department of Interior, owns the land, methods should be investigated to solve not only the grazing problems, but also the water deficiencies that presently exist on the refuge. Stillwater NWR is unique in that it provides marshland habitat in an area that has few wetlands.

Summer grazing continues, although at a greatly reduced level from 1975 and 1976, on Grays Lake NWR, Idaho, even though the endangered Whooping Crane is presently being introduced by transplanting their eggs into Greater Sandhill Crane nests. In 1975 two young Whooping Cranes disappeared within 2-3 days after large numbers of cattle were introduced into areas occupied by these chicks.

Improvements have been made on some refuges. Hart Mountain NWR, Oregon, began reducing AUM’s in 1969 and in 1976 (11,000 AUM’s) the number of pronghorn antelope young per 100 does was 59. On Sheldon NWR, Nevada (24,000 AUM’s), immediately south of Hart Mountain NWR, the young-adult ratio was only 22/100 (E. McLaury, pers. comm.). Present plans are to reduce the number of AUM’s at Sheldon.

At Bosque del Apache NWR, New Mexico, all grazing has been terminated. All internal fences have been removed and many pastures which had been “improved” for cattle have been converted to wildlife food crops or man-made marshes. Wintering Snow Geese (Chen hyperboreus) have increased from a few hundred to over 21,000 in the past 10 years and Greater Sandhill Cranes have increased from 3200 to over 12,000.

At Ruby Lake NWR, Nevada, grazing occurs from 15 April through 1 January. Present plans are to reduce the 5200 AUM’s by one-half. Wildlife changes that occur in the deferred and hayed-only areas will be monitored and compared with those in areas that continue to be grazed.

At Red Rock Lakes NWR, Montana, the management announced to local stockmen that there would be a 10% reduction annually in AUM’s over a 5 year period. Surprisingly, little opposition was encountered and the program is in its third year, with AUM’s now 30% fewer than the original 13,144.

Prescribed burning has been used in grassland management to maintain desired successional stages. To avoid the cost of fencing, issuance of permits, soil erosion, overfertilization (affecting water quality), and other aspects of grazing programs, burning could be used to accomplish the same objectives. This would also prevent the refuge system from becoming more involved with and influenced by local stockmen, grazing associations, and political pressure (Voight 1976).

Haying

In 1974-75, 16,714 ha were mowed for hay but ungrazed by 589 permittees on National Wildlife Refuges. In comparison with grazing, haying generally creates only minor conflicts with wildlife management. The 3 major grazing states had minimal hay acre-
ages in 1974–75. The Central Flyway was most important, with refuges in North Dakota (4521 ha) and Nebraska (4185 ha) being leaders in this practice (USFWS 1976b).

In some situations haying can be beneficial. Native grasslands that receive flood water in late spring can be mowed to discourage early nesting species. In areas with limited water supplies, channels can be mowed to allow for rapid water movement. Data from Malheur NWR, Oregon, have shown that Greater Sandhill Cranes, Canada Geese (Branta canadensis) and some species of ducks, feed and loaf in mowed areas, but prefer to nest in unmowed areas.

The major conflict with mowing is the time of year when it begins. Interviews with mower operators on private land in southeast Oregon in 1976 indicated high mortality of young birds from 1 to 15 July. Two operators estimated they had killed between 400 and 600 birds during this 2-week period. Most of these were shorebirds, but numerous waterfowl nests, young ducks, and crane chicks were also reported destroyed. One operator stated that he had killed 2 pronghorn antelope young in 1975. On Malheur NWR, 4.2% of the Mallards hatch after 16 July. Other species and hatching percentages are: Gadwall (Anas strepera) 14.5%, Cinnamon Teal (Anas cyanoptera) 15.0%, and Redhead (Aythya americana) 13.4%. Many newly hatched broods are seen after 1 August. Younger Greater Sandhill Cranes suffer high mortality from mowing, especially early in the season. Young cranes lie down and hide in vegetation when approached and remain hidden until hit by the mower. Recently at Malheur NWR, haying has been delayed until 10 August to allow cranes time to fledge. In some areas on the refuge where flightless young are known to occur, mowing has been delayed even longer.

Many refuges begin mowing activities in July, with some possibly as early as late June. Until recently Medicine Lake NWR, Montana, initiated mowing on 15 June. Because of political pressure from one permittee, it was about 8 years before mowing was terminated after it was publicly announced that it was to be stopped within 2 years.

Data collected at Malheur NWR is potentially applicable to other waterfowl production areas. Refuges that allow mowing before 1 August are contributing to substantial losses of wildlife. Biological data on the effects on wildlife should be collected on refuges that have early mowing programs. To alleviate losses, having should be delayed until 15 August. It is important to note that virtually no data are available regarding the impact of haying (or grazing) on other ground nesting birds.

Farming

Farming for production of cereal grains for waterfowl use has long been a major endeavor on many refuges. Other crops (including oranges!) are sometimes grown. In 1974 at least 131 refuges farmed about 65,966 ha (USFWS 1976b). Primary reasons for farming on refuges relate to providing supplemental foods for waterfowl during migration and wintering periods and for preventing crop damage outside refuge boundaries. The latter has not been overly successful when the large concentrations of waterfowl, especially geese, cranes, and ducks on some refuges are considered. Farming practices on refuges have been successful in concentrating birds, frequently too much so as witnessed by problems with shortstopping birds before traditional wintering areas are reached, crop damage problems adjacent to refuges, hunter firing lines leading to such problems as lead-poisoning dieoffs and slob behavior of hunters, and outbreaks of density dependent diseases such as fowl cholera and duck viral enteritis. Possible negative side effects of farming on National Wildlife Refuges may result from crop associated use of pesticides and herbicides.

In the near past many refuges were evaluated on number of days of use they provided
for waterfowl. Consequently the pressure was to show yearly increases in numbers of waterfowl using areas over longer time intervals. It is now recognized by some refuge managers and administrators that these goals were not beneficial to the waterfowl resource. Consequently, amount of land farmed on some refuges is decreasing with diversification from cereal grains becoming apparent. Goals of refuges should be reevaluated. It is probable that having the bulk of individual populations of birds on one refuge for long periods, such as is common with geese, is not healthful for the birds or beneficial to the overall management of the resource. Diversified and well dispersed refuges, especially in migration and wintering areas, are most desirable.

**Timber management**

Management of timber for the lumber and pulp industries on National Wildlife Refuge lands occurred on 21 refuges, primarily in the southeast and northeast in 1974. These 21 refuges reported a timber harvest from 12,141 ha (USFWS 1976b). While this may be a small portion of the overall refuge system, impacts on some refuges are extensive. As an example of the magnitude of these activities, the annual operating budget for Noxubee NWR, Mississippi, has in recent years been about $110,000, yet this 13,760 ha refuge has sold up to $250,000 worth of timber per year. The income goes into the Federal Treasury and does not come back to the refuge system. Timber management and some economic gain from the forests on National Wildlife Refuges is not inherently bad. The extent and type of management may be. For example, the USFWS slogan used to characterize timber management on southern National Wildlife Refuges is “all-age management in even-age units.” This is a euphemism for clear-cutting. A booklet describing this management system on Noxubee NWR states: “The highly productive alluvial soils (growing mostly hardwood) are managed under a long rotation (120 years) and a frequent cutting cycle (15 years). The rotation age for upland areas (including both pine and hardwood) is 80 years, and a cutting cycle is 10 years.” Thus, “all-age management” allows some hardwoods to grow to the age of 120 and some pines to grow to the age of 80. If such a plan was truly for “all-age” management, the rotation cycle should be based on the natural potential longevity of the trees involved. Sizes of clearcuts are stated in USFWS brochures to be limited to 12 ha though refuge foresters admit that some cuts approach 20 ha. Aside from rotation ages and sizes of cuts, there is enough controversy over the ecological effects of clearcutting (decreased diversity, etc.) that this practice seems inappropriate for management of a National Wildlife Refuge. In short, the forests of National Wildlife Refuges in the southeast are being managed to maximize economic return at the expense of those wildlife species such as Red-creckaded Woodpeckers (*Picoides borealis*) which require more mature forests. An important component of the southern forest ecosystems is being lost.

**Predator control**

Few data are available on predator problems on National Wildlife Refuges. In 1972 predator control through use of toxicants was discontinued on most public lands. Unfortunately, few comparative data were collected before 1972, and on most refuges little has been collected since 1972.

It is possible that many refuges have only minor predation problems, but some have high predation rates. Data have been collected on Greater Sandhill Cranes on Malheur NWR, Oregon, since 1966. After predator control through poisoning was terminated in 1972, production was greatly reduced from 1973 through 1975. From 236 pairs that nest on the refuge, only 2 young fledged in both 1973 and 1974. In 1975 only 17 fledged.
Common Ravens (*Corvus corax*) and raccoons (*Procyon lotor*) were the major egg consumers, while coyotes (*Canis latrans*) took eggs and young. In the winter of 1972–73 the black-tailed jackrabbit (*Lepus californicus*) population sharply declined and coyotes moved onto the refuge to find alternate food sources. One pond where more than 300 young Canada Geese were captured and banded in 1972 produced only 28 in 1973. It was not uncommon during mid-day in August to observe more than 45 coyotes along one 68 km road through the refuge. Coyotes normally cause only minor problems on Malheur when jackrabbit numbers are high. However, Common Ravens find ideal conditions in southeast Oregon. Numerous rimrocks provide nesting sites and the cattle industry and nesting birds provide an abundance of food. One roosting site on Malheur Lake in 1976 was being used by more than 800 ravens.

Two noteworthy predation incidents were documented in 1976. At Crescent Lake NWR, Nebraska, 2 of 5 Trumpeter Swans (*Cygnus buccinator*) that were to be released in 1977 were killed by raccoons or coyotes, and 26 Greater Sandhill Crane nests including 3 that contained transplanted Whooping Crane eggs, were destroyed by coyotes at Grays Lake NWR, Idaho. Predator problems have also been reported at Attwater Prairie Chicken NWR, Texas.

Many refuges are artificially developed with numerous canals, artificial ponds, nesting islands, water control structures, and other man-made elements to attract waterfowl and other birds and encourage nesting. Such an artificial environment also attracts large concentrations of predators, especially when predator control is being practiced on surrounding private lands. With habitat manipulation, species that require dense nesting cover are benefitted. But for species that nest in open situations and construct nests that are exposed during periods of absence, dense vegetation is of little value, and nests are especially vulnerable to avian predation. Many species of shorebirds and marsh birds fall into this category. On refuges that support breeding populations of species with low reproductive potential, predator management should be used to insure their continued survival.

Severe losses on some refuges will continue if predator populations remain unchanged. If nesting studies are not initiated to ascertain the impact of predation, present practices of non-control will continue. Whether California Gulls (*Larus californicus*) in Utah, Black-billed Magpies (*Pica pica*) in Colorado, striped skunks (*Mephitis mephitis*) and red foxes (*Vulpes fulva*) in North Dakota, Common Ravens in Oregon, etc., the impacts of predators on federal wildlife refuges need to be examined. If predators are a serious detriment to the production of other wildlife, their populations should be properly managed.

**Recreational activities**

_Fishing._—In 1974 fishing was allowed on 171 refuges with fishing waters being stocked on at least 18 refuges (USFWS 1976b). Generally fishing is a recreational use of refuge wetlands that is compatible with the protection and management of birds. However, excessive use of shallow vegetated areas of lakes and streams by wading and boating fishermen can disturb feeding and nesting waterbirds. Many southern refuges, such as Noxubee NWR, prohibit fishing during the winter months in order to provide sanctuary for wintering waterfowl, though when nesting activities of resident species are beginning, the lakes are opened to fishing again. Prime nesting areas on many refuges are closed to fishing until about 1–15 July. Such dates are unrealistic on some refuges as nesting continues after these dates. Timing of fishing closures (if any) varies from refuge to refuge and no policy appears to have been formulated on this use of refuges above the
local level. In northern areas, fishing should be delayed until about 1 August with some presently open fishing waters being closed to protect late nesting species and their broods. In general fishing regulations on refuges are appropriate but some refuges allow use of trot lines upon which mergansers, loons, and diving ducks have inadvertently been snared. This is an unnecessary abuse of National Wildlife Refuges.

**Boating.**—Various sizes and types of boats have been used on National Wildlife Refuges for many years in pursuit of refuge management goals and fishing. With the advent of motors and more leisure time, various publics have demanded and received access to National Wildlife Refuges for motor boating and water skiing. Presently 42 refuges permit high speed pleasure boating; mostly on areas where the USFWS has secondary control (USFWS 1976b). Obvious and documented impacts of high speed boating are shoreline degradation, disruption of nesting and feeding areas with loss of production of young, and displacement of water birds. These problems, especially loss of production of young, are especially pronounced at Ruby Lake NWR, Nevada, and have resulted in the preparation of an Environmental Impact Assessment on the effects of boating at this refuge (USFWS 1976a).

Ruby Lake NWR was established 2 July 1938 as a refuge and breeding ground for migratory birds and other wildlife. Most of the 15,229 ha area was purchased, with the remainder being withdrawn from the public domain. Boating was allowed for the purpose of fishing starting in the mid-1940's, with water skiing being allowed starting about 1955. Sizes of boats and motors and numbers of water skiers increased until the late 1960's when the USFWS moved to protect the waterfowl resource (principally nesting Canvasback, Aythya valisineria, and Redhead ducks) by restricting power boating. Since that time public and political pressures have prevented adequate restriction of power boating necessary to protect the waterfowl resource with concomitant decreases in production of over water nesting waterfowl. More recently commercial developments by large corporations have resulted in a proliferation of sub-divisions for recreational homes in the area near the refuge. Advertisements clearly indicate that Ruby Lake NWR and associated water related activities on the refuge are important inducements attracting people to purchase "ranchettes," etc. With increasing political and public demands for boating related activities on this refuge, it is quite obvious that the original purpose of the area has been lost. The future of this refuge is in dire straits and it may become a recreation area if public apathy cannot be changed to prevent local abuse of a national resource.

Boat related disturbances with no or little consideration of values of wetlands and associated water birds have no place on National Wildlife Refuges. When threatened or endangered species are impacted by such activities, closures of refuges to boats should be mandatory.

**Hunting.**—Sport hunting of wildlife was permitted on portions of 184 National Wildlife Refuges in 1974 (USFWS 1976b). Hunting was primarily for migratory waterfowl but also was allowed for resident game birds and big game species. Since hunters have provided funds for much of the prime wildlife habitat purchased for refuges, it is logical and rational that some level of hunting be allowed. Few refuges are completely open to sport hunting and it would appear that state and federal regulations on season length, bag limits, methods of taking, etc. are more than adequate to maintain avian resources. Where endangered species are involved, such as Whooping Cranes and Mexican Ducks (*Anas diazi*), it is difficult to see the rationale for sport hunting of look-alike species. Hunting of look-alike species on those few refuges where these potential problems exist should necessarily be reevaluated and probably discontinued.
Other management problems

A recurring problem on National Wildlife Refuges is the ease with which refuge lands can be abused by other federal agencies. Some refuges have been used as practice areas for low flying military aircraft, others as convenient and inexpensive routes for highway and utility rights-of-way. The advent of NEPA hopefully will eliminate some of this abuse, but problems still remain. For example, the USFWS had no objection to the channelization of the Yazoo River by the U.S. Army Corps of Engineers through Yazoo NWR, Mississippi.

A recent trend in refuge management has been to consolidate land holdings and to adjust refuge boundaries to facilitate management. This has the effect of making a nice compact refuge rather than one with “fingers” extending into the surrounding non-refuge lands. While we appreciate the management problems involved, such consolidation often results in losses for wildlife. At one refuge the adjustments in land holdings were made by trading prime forest land for agricultural lands. In addition to the loss of not-soon-to-be-replaced forest habitat, the deal also resulted in a net loss in acreage to the refuge. Apparently it is easier to trade lands than it is for a refuge to either sell or purchase lands. Hence, based on market values, the refuge traded more acres of forest to obtain fewer acres of crop land. We feel that the increased edge and linear distances on more dispersed refuges can often provide habitat for larger wildlife populations than could compact refuges. An added benefit of such dispersed refuges is that they often provide an ecological archipelago that will allow wildlife the opportunity to disperse to other suitable habitats outside the refuge.

Some National Wildlife Refuges include areas of potential value as wilderness. Such areas should be identified and protected. Personnel at one refuge indicated that such an area occurred on their refuge, but that they were going to construct a road through the middle of it so that it would not qualify for wilderness status and so that current forest management practices could be continued. Such actions are deplorable.

In addition to management or lack of management on National Wildlife Refuges that affects birds, we feel compelled to point out a few refuge “management” practices that adversely affect ornithologists and bird-watchers. Refuges tend to be generally understaffed as a result of inadequate funding. One reflection of this problem is the operating schedule for most refuges. Refuge offices typically open at about 08:00 and close about 16:30 Monday through Friday and are closed on weekends. This is fine for carrying out wildlife management activities, but many refuges also receive large numbers of human visitors—most on weekends and after regular working hours. An open office with descriptive brochures and bird checklists could win a lot of support for the refuge system. Additionally, as some refuge managers see it their biggest problems are managing people. Perhaps these management problems would be fewer if refuge public relations were improved by tailoring refuge office hours to accommodate visitors and by providing informational materials.

Ornithologists seeking to conduct ecological research on National Wildlife Refuges are faced with an unwarranted number of bureaucratic problems. Not only are state and federal bird banding permits required, but the researcher must also obtain a refuge permit and file an annual report of his activities on the refuge. If permits were simply obtained by visiting or writing to refuge headquarters, the requirement would not seem unreasonable, but often this is not the case. Permit requests are often channelled through regional USFWS offices, sometimes through Washington, D.C., before a permit is granted—thus causing the researcher loss of valuable time. Collecting permits for refuges are particularly difficult to obtain—and perhaps justly so, were it not for the fact that
hunters are often given freedom to hunt game birds on refuges with no more difficulty than obtaining a state hunting license and a duck stamp. Another problem associated with conducting research on National Wildlife Refuges is the USFWS practice of frequently moving personnel from one refuge to another. As soon as a researcher has established a good working relationship with one refuge manager, he is often confronted with explaining his work and adjusting his research activities to conform to a new manager’s interpretation of regulations. In all fairness, however, the legitimate ornithological researcher has much to gain from working on National Wildlife Refuges. Our experience has for the most part been that refuge personnel are eager to have research conducted on refuges and that they are willing to provide logistic support whenever possible.

SUMMARY

National Wildlife Refuges administered by the U.S. Fish and Wildlife Service, Department of Interior are located in 49 of the 50 states and encompass more than 13,678,860 ha. While purchased or obtained for a variety of purposes including migratory birds (primarily waterfowl) and endangered species, National Wildlife Refuges are vitally important for maintenance of important habitats and overall conservation of many species of birds. Problems associated with management of National Wildlife Refuges include: (1) concentrating large numbers of birds which increases risk of catastrophic losses due to disease and other mortality factors and the opportunity for damage to items valued by man; (2) overgrazing by domestic livestock; (3) cropping for hay; (4) water oriented activities such as boating; (5) creation of monocultures by selective cropping or planting practices; (6) a lack of selective management of predators; (7) failure to consider impacts of artificial structures such as fences, powerlines, signs, etc.; and (8) inadequate manipulation of biological and mechanical tools useful for maintaining and improving habitats useful for birds. Major administrative problems include failure to clearly identify and support objectives of individual refuges and woefully inadequate funding for refuge staffing and maintenance.

RECOMMENDATIONS

1. Creation of a National Wildlife Refuge Service equal to the U.S. Fish and Wildlife Service in the Department of Interior to manage National Wildlife Refuges would result in unnecessary bureaucracy, diversion of talent and funding, and would fragment a cohesive national policy for protecting habitat for wild animals. Administration and management of National Wildlife Refuges should continue as a function of the U.S. Fish and Wildlife Service, Department of Interior. However, the refuge system should be given full program status and administration should be streamlined with an Assistant Director directly responsible for the refuge program.

2. Funding for staffing and maintenance of National Wildlife Refuges has been woefully inadequate for many years. Adequate funding to maintain refuges should be strongly supported. Funding for enhancement of existing refuges is desperately needed as is funding for expansion of the refuge system. Funding should be increased for public relations and hiring of non-game biologists.

3. Objectives of each National Wildlife Refuge should be reevaluated with management being directed towards obtaining desired objectives once they are defined.

4. Uncontrolled grazing by domestic livestock has been documented to adversely affect nesting success and productivity of birds. Grazing of domestic livestock on National
Wildlife Refuges should be carefully evaluated and in many instances reduced to levels compatible with refuge objectives. Proper timing of grazing is critical and all summer grazing in production areas should be eliminated. Winter grazing should be allowed only for desirable habitat manipulation where controlled burning is not feasible. Refuges should not be managed for domestic livestock production.

5. Controlled burning has value for manipulating habitats and it should be further tested with effects documented. Where beneficial, controlled burning should be used in refuge management.

6. Unnecessary structures such as fences, powerlines, etc. should be removed within refuge boundaries where they have been documented to be hazardous to birds. All necessary structures should be marked with aircraft warning markers or other devices to prevent and reduce bird-object collisions.

7. Mowing of habitats for hay crops or other refuge objectives should be delayed until 1-15 August in production areas important to birds. Dates of mowing after 1 August should depend on locality and local condition. Management of refuges for commercial hay crops is not desirable.

8. Selective control of predators on refuges managed for birds should be implemented in areas where limited nesting and brood cover occurs or where severe local conditions exist. Management of production refuges should seek to prevent ecological situations favorable to maintaining or encouraging unnatural concentrations of predators.

9. Excessive or unnatural fall and winter concentrations of birds should be discouraged through habitat manipulation on refuges; such concentrations invite catastrophic losses and damage to private property.

10. Public recreation activities on National Wildlife Refuges should not be given preference over stated objectives of the refuges. Examples of undesirable activities when birds are nesting are boating, water skiing, and fishing. Non-human use areas are an integral part of the refuge concept and all human recreation activities should be meshed within the objectives of each refuge. Public visitation should be encouraged on portions of refuges with adequate staffing and suitable open hours.

11. Diversity of habitats should be encouraged on National Wildlife Refuges and practices that lead to large areas of monoculture should be discontinued. This is especially a problem in forested areas.

12. Forest management on National Wildlife Refuges should take into account the natural potential longevity of the tree species present and should provide for the needs of species characteristic of mature forest ecosystems.

13. Collection and compilation of data concerning the effects of management practices on avian species, especially non-waterfowl, should be an integral part of refuge management. Research into management procedures and other scientific endeavors should be encouraged on National Wildlife Refuges with improvement of permit procedures and requirements being immediatelyinstigated.

14. Consideration should be given where feasible to include portions of some refuges in the Wilderness System to further protect unusual and unique habitats.

ACKNOWLEDGMENTS

The volume of correspondence generated by interest in this topic was considerable. We thank all who corresponded with us and hope that confidences were not compromised. Numerous personnel of the U.S. Fish and Wildlife Service assisted us in locating literature references and in providing access to unpublished refuge reports. These individuals
are dedicated to maintaining and enhancing wildlife habitats despite administrative harassment, snafus, and inadequate funding. We are indebted to them and are sincerely appreciative of their efforts. Special thanks go to E. M. Brigham, III, R. Drewien, C. E. Knoder, G. L. Pearson, and C. Talbot for constructive suggestions and comments. While many individuals discussed the topic with and in other ways assisted us, the report and recommendations were prepared by the Conservation Committee and represent our collective position.

LITERATURE CITED


Conservation Committee
Clait E. Braun, Chairman
Keith W. Harmon
Jerome A. Jackson
Carroll D. Littlefield
ORNITHOLOGICAL LITERATURE

Rails of the World. By S. Dillon Ripley, illus. by J. Fenwick Lansdowne. Chapter on fossil species by Storrs L. Olson. David R. Godine, Boston, 1977:xx + 406 pp., 41 color plates, 35 black-and-white plates, 17 maps; size 10 $\times$ 14 in. $75.00$.—Dillon Ripley has been interested in rails since his earliest expeditions abroad many years ago, and has long wanted to write a monograph on the family. He was both inspired and challenged by Alfred Newton’s remarks in the Dictionary of Birds (1893) that the rails are an enigmatic and little known family for which a monograph would prove rewarding and valuable. Ripley further explained his purpose in a meeting at the Peabody Museum in 1977, as quoted in Discovery 12(3):44 (1977), that he had become certain over the years “that if I ever could write a monograph on the rails, not only had one never been written before, but the likelihood was that one would never be written again, and that almost anything I managed to say about the rails was likely not to be very strongly corrected in the future, so that I had clear sailing by taking on a family that is as obscure, and little known, and enigmatic as the rails.”

The result of Ripley’s endeavors is a handsome monograph that certainly can take its place in the parade of fine bird books of recent years. This is a book in the grand manner; large, lavishly illustrated, and printed on fine paper with wide margins. It combines the attributes of a “coffee table” book that is a pleasure to browse through, and a utilitarian work of inestimable value to all who are interested in rails.

Fenwick Lansdowne is an accomplished artist whose rails here are generally successful and attractive, though a few have the wrong shape or pose. The Spot-flanked Gallinule is drawn to look like a gallinule, which it is, but in the field it looks like an oversized Porzana, and its bill is much brighter than pictured here. One irritating thing about the paintings is that the birds are not drawn to scale. On the first plate, for instance, the giant bird in the middle of the picture is Eulabaeornis castaneoventris, length 11 in., while the small one crouching at the top left corner is Himantornis, a hefty 17-inch bird. There are many other examples of this lack of scaling. The grouping is sometimes curious. Two Canirallus are on Plate 2 with Wallace’s Rail, while the third is on Plate 3; why not put all 3 together? Perhaps the artist did the plates before the taxonomist started playing around with the genera. Another irritation is that while the text is keyed to the plates, the reverse is not true. The plate captions should have contained page references to the species accounts. Despite these annoyances the plates are a fine addition to the book and make a large contribution to its success.

The book is divided into an introduction and 5 parts. In the introduction Ripley gives a history of the discovery of rails, written with a charming antiquarian flavor, and describes his own early involvement with the family. His pleasant writing style makes for easy reading.

The acknowledgments come at the end of the introduction. From the vague generalization that “in recent years Gorman Bond and Michel Desfayes have undertaken further to make this whole work possible for me,” one would never guess that what these 2 really did was to research and write up much of the data for the present work. Ripley should give proper, specific credit where due.

Part 1, The Characteristics of Rails, has sections on anatomy, classification, locomotion, flight, nesting, voice, duetting, display, fighting, and various aspects of the relationships between rails and man, with a long section on hunting. In the classification on p. 5, only 3 of the 8 promised gruiform suborders are listed; the other 5 were somehow left out.
The section on classification deserves some comment, mainly because of Ripley's radical revision of rail genera. His classification can be compared to those of previous authors as follows:

<table>
<thead>
<tr>
<th>Genera</th>
<th>Species</th>
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<tr>
<td>Sharpe (1894), Catalogue of the Birds in the British Museum, vol. 23.</td>
<td>50 165</td>
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<td>Peters (1934), Check-List of Birds of the World, vol. 2.</td>
<td>52 138</td>
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<tr>
<td>Berndt &amp; Meise (1960), Naturgeschichte der Vogel, vol. 2.</td>
<td>51 138</td>
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<td>Fisher &amp; Peterson (1964), The World of Birds.</td>
<td>51 130</td>
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<tr>
<td>Olson (1973), A Classification of the Rallidae, Wilson Bull. 85:381-416</td>
<td>35 ?</td>
</tr>
<tr>
<td>Ripley (1977), Rails of the World.</td>
<td>18 129</td>
</tr>
</tbody>
</table>

It can be seen that while Ripley has made few changes at the species level, the carnage among the genera has been great. While few would deny that the time had come to do away with many of the old monotypic genera, one wonders whether such wholesale slaughter is really justified. There is no doubt in Ripley's mind that it is, for he says (p. 6) "I find few of the reasons advanced for maintaining additional genera compelling or cogent. A single question... seems to me open to arguments of taxonomic taste or discretion." In other words there is only one correct treatment—his own. Attention, rail taxonomists! The final word has now been spoken. You should be looking for work in other fields. Ripley continues: "For the rest, the preservation of so many genera of rails up until now has been a question of waiting for monographers to address themselves to this neglected family." This is true, but the reader should not get the impression that Ripley was the pioneer monographer who made the break with tradition. That pioneer was Storrs Olson, who reduced the number of genera to 35. Incredibly, Olson's classification is not even mentioned in the list of previous classifications on p. 6. Here is another instance of proper credit not being given.

In part 3, Evolution and Speciation, Ripley gives his reasons for merging various genera. Arguments will probably continue forever as to what constitutes a valid generic character, and every taxonomist is entitled to his own opinion, the only requirement being that he be consistent in his use of characters. The same character must not be used for 2 opposing functions. While many of Ripley's generic limits seem reasonable, he is sometimes guilty of this no-no. Thus, plumage similarities are the basis for merging Neocrex in Porzana and Aramides in Eulabaeornis, while plumage dissimilarities are ignored in uniting the African genus Sarothrura with the totally dissimilar New World genera Coturnicops and Micropygia. This arrangement is in any case geographic nonsense; and no-one who has ever heard the voices of both the Yellow Rail and Sarothrura spp. would ever dream of putting them in the same genus.

Part 2, The Distribution of Rails, is the most successful of the introductory sections, concentrating on the causes of distribution and covering subjects like adaptation and dispersal. Among other topics Ripley discusses the reasons for the success of rails as colonizers, and shows how their reluctance to fly and their rapid evolution of flightlessness might paradoxically help rather than hinder colonization. This is a thought-provoking and well-written section.

Part 4, The Species of Rails, contains the species accounts. This is the real meat of the book and its most valuable contribution. It is prefaced by a key to the genera, while in the text the genera have species keys and the species have subspecies keys. Each species account contains a brief overall description of the bird, taxonomic comments, and
a discussion of habitat, voice, food, and breeding. Each subspecies account contains a detailed description, measurements, distribution, and status. There are only 17 maps, and these are reserved for polytypic species with the most complex distributions. The maps are well-drawn, clear, and easy to read. There is a tremendous amount of information here, and the researchers evidently did a good job with the literature since the text is freely littered with citations. While excellent as regards “museum” type information (description, measurements, subspecific characters, distribution, etc.), the text would have benefitted from more first-hand field experience of the writers. Lacking this an attempt should have been made to contact other workers in the field and obtain unpublished information from them. In the account of Rallina tricolor, for example, out of nearly 2 full pages of text there are just 3 lines on life history as follows: “From the little that is known of its life history it appears to share the ralline habits of secrecy and stealth, damp habitat, and crepuscular calling and feeding preferences.” You could make this same statement about most of the rails of the world and get away with it. Yet there is specific information about the bird. In 1974 Mrs. H. B. Gill, a well-known Australian amateur ornithologist, took me to see a pair of Rallina tricolor inhabiting a stream near her house. I taped the calls and played them back, which brought the birds into view. But I was not witnessing something new to science. Mrs. Gill had kept the birds under observation for some time and had already shown them to a number of visitors. Here was a paragraph of information on the species just waiting to be tapped. Also, there are only 2 lines on status in the entire account: “By no means rare in Queensland (E. P. Ramsay in Mathews, 1911).” Surely more is known about its status than a single remark in a book written 66 years earlier. Again, the status of Canirallus k. kioloides is given as “Especially common on the narrow coastal plain at Maroantsetra (Rand, 1936).” That may have been true in Rand’s day, but today most of the vegetation there has been cut down and does not harbor Canirallus, as Ripley could have discovered by checking with recent workers in Madagascar. Rouget’s Rail, Rougetius rougetii is said to “keep hidden in thick vegetation during the day,” and appear at dusk and dawn, another safe statement about almost any rail, but this one is a maverick and comes boldly into the open far from cover during daylight hours. I have sat in my car on the main highway north of Addis Ababa and watched Rougetius feeding on bare mud by a small pond, scarcely blinking as trucks and buses hurried by. The above instances only indicate a certain lack of field experience with the birds concerned and a lack of depth in research, and should not obscure the overall value of the information presented.

While the species accounts fulfill their function of drawing together information from every source, there is also new information of interest. Ripley has stuck his neck out and lumped King and Clapper rails, a treatment that will annoy many while pleasing others, but Ripley has bolstered his case with a lot of data, including personal communications, and has produced a reasonable argument. Again, there is a lot of information on the Galapagos Rail, Laterallus spilonotus, derived to a great extent, it would seem, from an unpublished MS by Alan Franklin and Deborah and David Clark, who studied the bird in the field. Strangely, there are no taxonomic comments on this bird, which has hitherto been considered a subspecies of the Black Rail, Laterallus jamaicensis. While this separation may well be justified, I think we are owed an explanation.

Part 5, A Synopsis of the Fossil Rallidae by Storrs L. Olson, is worthy of high praise. It is much more than a simple catalog. Each species is written up under the following headings: Holotype, Horizon, Locality. Material, Illustrations, and Remarks, the latter often containing considerable discussion. The chapter is copiously illustrated with
photographs and drawings of bones. This is a most valuable contribution by one of the world’s leading authorities on the subject.

In conclusion, despite many faults this is a worthwhile and valuable publication. To have put all the rails of the world between two covers, complete with illustrations, is a praiseworthy achievement in itself. The price is steep but not out of line with today's incredible book prices, nor unreasonable considering the quality of production and number of illustrations. For all who can afford it, I can certainly recommend the book.—Stuart Keith.


The Audubon Society Field Guide to North American Birds. Eastern Region. By John Bull and John Farrand, Jr., Alfred A. Knopf, produced by Chanticleer Press, New York, 1977:775 pp., 584 color photos. $7.95.—A bird guide that tops the New York Times Book Review best seller list for paperbacks (which it is not) for several weeks, and which remains on that list for several months deserves more than passing mention. The dust jacket claims the book to be "a revolutionary field guide. Unique on four counts." The supposed novel ideas are to illustrate the various species with color photographs rather than paintings, a "visual organization" of these photographs by color and shape, and a text arranged by habitat. None of these ideas is really new. The argument as to whether a photograph or a painting is the best means to present a typical representation of a bird is an old one (see a review by R. Mengel, Auk 72: 308–310, 1955), and in this case our authors, both connected with the American Museum of Natural History, come out wholeheartedly for photographs, "every artist rendering of a bird is his interpretation whereas a good photograph captures the natural color and stance of birds as you usually see them" (p. 12). The operative word is, of course, "good."

The extent of the participation of the Audubon Society (National) in the preparation of the book is nowhere made clear, although Susan Rayfield of the staff of Audubon is listed as "Project Editor" and is given credit for the development of the "Visual Key." I understand that it was she who performed the herculean task of rounding up the photographs used. In some ways this guide shows signs of lineal descent from the "Audubon Guides" written by Dick Pough a generation ago. Much the same geographical range is covered (everything east of the Rocky Mountains), and the present work attempts as did Pough to provide information beyond simple identification matters.

There are 584 color photographs covering 456 species. Most species are represented by spring males only, but 122 species have a second illustration, usually of a female or of another plumage. Twenty-six species are described but not included in the photographs, although a very small drawing of these species accompanies the text.

The photographs are clumped in the first half of the book, arranged in groups of similar shape, with small silhouettes serving as location guides. The passerines are arranged by color. The 2 photographs of dimorphic species are thus often widely separated. Arrangement by color also meant that some arbitrary decisions had to be made as to under what color to include a given species. These decisions were sometimes rather unwise, as for example the predominately gray and yellow Western Kingbird is listed under green birds. The text accounts of the species are arranged under 12 categories of habitat. Here again arbitrary and not always fortunate decisions had to be made. The Great Horned Owl, which must nest in almost any habitat, is listed under "Coniferous Forest," the Red-headed Woodpecker is listed under "Grasslands" and inland birders
will be somewhat at a loss to find many familiar ducks listed under "Seashores." Usually these inconsistencies are set to rights in the text description of habitat, however.

Several appendices are included: thumbnail sketches of the avian families occurring in North America, a brief essay on bird watching, a glossary, a list of endangered species, and a list of photographic credits. The arrangement of this latter list makes it very difficult to find out which photographer gets credit for a particular picture.

The color pictures deserve critical comment. Color reproduction on a mass basis has come a long way in recent years and the job done here is an outstanding one. At the moment I know of no other collection of beautiful color photographs of birds that can be obtained so cheaply. Most of the pictures are excellent, although a few show unusual or even distorted poses. I could detect very few color distortions in my copy. The delicate sky-blue of the Mountain Bluebird and the Lazuli Bunting have reproduced to look more like the harsher blue of the Indigo Bunting and some of the other blues are slightly off. None of the plates in my copy is out of register.

A few of the pictures are bad, however, with the nadir being possibly the Philadelphia Vireo (451), and a number of others, while not bad as photographs, fail to show field marks of aid in identification. Examination of some of the pictures used, as well as the list of species not figured would indicate that even today some of our North American birds have not been adequately photographed. The Philadelphia Vireo may fall in this category. Unfortunately, there are some errors in identification. Plate 387 which is supposed to represent the presumably rarely photographed Black-headed Oriole (*Icterus graduacauda*) is actually one of the Old World orioles, possibly *Oriolus larvatus* which is also known as the Black-headed Oriole. Plate 268 is a female Spruce Grouse rather than the labeled Ruffed Grouse and Plate 37 appears to be a Western Gull rather than the indicated Herring Gull.

A definite hazard of using photographs for a field guide comes from the fact that many species are most commonly photographed on the nest or at least on the breeding grounds, and for some species the full breeding plumage is rarely seen by most bird watchers. Thus, the very fine picture of Sabine’s Gull (44) at the nest would be of little help in identifying a winter-plumaged bird off the Maryland coast. Similarly, phalaropes in breeding plumage and alcids in close view are seldom seen by birders. Perhaps the most flagrant example of this is the Ruff (Plate 214) in its elaborate breeding plumage, photographed in full display, a charming and interesting picture but one bearing practically no resemblance to any Ruff ever seen on this side of the Atlantic.

From many years of experience in showing beginning bird watchers live birds in the hand at banding stations, I have become aware that often the tyro is overwhelmed by the detail in the plumage patterns. This hazard is also prevalent in the current guide. The duck pictures are by and large the most beautiful I have ever seen, but the detail of the feather patterns, the fine vermiculations, and the play of colors evident in these pictures are certainly not apparent when viewing ducks across an expanse of choppy water on a rainy, windy day.

All of the birds in the photos are reproduced to the same size, and even though a measurement of length is given for each species I fear that incongruous size relations will hinder rather than help the tyro. Some of the backgrounds in the pictures are unfortunate, the most ludicrous being a Chimney Swift posed awkwardly clinging to the side of a smooth-barked tree.

We are on surer ground when we consider the text. Both of the authors know their bird identification and they do a good job of describing the salient features for identification in the brief paragraphs allotted to this point. A few inconsistencies do occur. For example, on page 651 we are told that the Mourning Warbler lacks an eyering, but on
page 706 we learn that it does have one. To add to the confusion the male in the photograph (372) does not have one but the female in the same photo does. In fact, many Mourning Warblers, particularly fall females do have at least a partial eyering, a character seldom mentioned in any field guide. An inconsistency of another sort comes when we are informed on page 638 that the Black-crested Titmouse is included under the Tufted Titmouse, but on page 613 it is considered a full species.

Besides the descriptions, the text entries for each species include a very sketchy description of the voice, and range descriptions that are so abbreviated as to be misleading in some cases, particularly those northern species that nest south along the Appalachians. There are also habitat descriptions that are generally adequate and as mentioned above go a long way towards correcting the misleading categorization by habitat, and a brief description of the nesting habits. At the end of each species account there is a short paragraph presenting some additional information about the species, ranging from the trivial, through the self-evident, to some worthwhile and interesting information. As with the habitat categories there appears to be some slight bias towards things of interest to coastal bird watching and some of the remarks fail to apply to the given species when found inland.

How then does this book in the final analysis stack up as a field guide? Regrettfully I must decide, “Not well, at all.” It will be a rare novice bird watcher who can identify any but the most obvious species (usually only males) with this guide. Such things as the grassland sparrows, the shorebirds, and particularly the raptors will be very difficult. The fall warblers would be impossible.

The classic advice to beginning bird watchers is to equip themselves with a good field guide and also a set of good colored pictures of the birds. I suggest that for the beginner this book is a very good one for the second purpose to go along with one of the better guides. It is true that he will have a hard time finding any particular species except by way of the index, but he can enjoy the pictures. For the experienced birder I would suggest that the price is right for a good set of color bird pictures. Indeed the experienced field birder might well profit by careful study of the detailed plumage characters shown in some species. On page 12 the authors say that the book is “—meant to be a delight to look at . . .” By and large this objective has been attained even if the book falls short in other respects.—George A. Hall.


The Pheasants of the World. 2nd Edition. By Jean Delacour. Spur Publications, Saiga Publishing Co., Ltd., Hindhead, Surrey, England, 1977: 395 pp., 33 plates, 21 text figures. £18.—This is an updated reissue of the standard work on pheasants, first published in 1951. The original text is reprinted without revision, but more recent information is included in addenda to the various sections. After a general introductory
account, each species is considered individually in terms of appearance, habits, distribution, and especially in relation to care and breeding in captivity.

In addition to numerous range maps, the book is handsomely illustrated with 32 plates painted by J. C. Harrison, half of them in color. Some of the quality of the original color plates has been lost in reprinting. There is a reduction in sharpness from the first edition, and some differences in color tones. Many plates have acquired a distinct greenish tinge. New to this addition is a frontispiece, an attractive painting of a male Himalayan Blood Pheasant by R. David Digby.

Anyone interested in pheasants, both in nature and in captivity, will welcome the reappearance and revision of this authoritative and visually pleasing work.—ROBERT J. RAIKOW.


**Species Relationships in the Avian Genus Aimophila.** By Larry L. Wolf. Ornithological Monographs No. 23, American Ornithologists' Union, 1977: viii + 220 pp., 10 pl., 17 figs., 36 tables, 1 long play record. $12.00 ($10.50 to A.O.U. members).—Even Robert Ridgway, who in 1901 established the genus Aimophila in its present form, felt that it was "a very heterogeneous and probably unnatural genus." Lack of information about the species in this genus has hampered attempts at arranging them into related groups, and a similar lack of information about many related emberizine finches has made intergeneric studies all but impossible. Dr. Wolf has added enormously to our understanding of relationships within Aimophila, but comparable studies of several possibly related genera are still needed, as are similar studies of the two South American species, *Aimophila strigiceps* and *A. (Rhynchospiza) stolzmanni*, which Wolf was unable to attempt.

This monograph contains a wide range of information on the 12 North and Middle American aimophilas, including geographic and ecological distribution, molts and plumages, territoriality and pair bond, foraging and food, vocalizations, breeding seasons, nest structure, egg color, external morphology, and skeletal characters. There is no list of specimens examined, but sample sizes on the tables indicate that more than 1100 study skins and 340 skeletons were examined, and weight data on 667 specimens were included.

Based on his analysis Wolf divides the genus into 4 complexes: the Haemophila complex (*ruficauda*, *sumichrasti*, *hameralis*, *myctalis*, and *carpalis*) having "radiated in the lowland scrub forests of western Mexico and the Pacific lowlands of Central America"; a *ruficeps* complex (*ruficeps*, *rufescens*, and *notosticta*) having radiated in "pine-oak woodland of Mexico and Central America," a *botterii* complex (*aestivalis*, *botterii*, and *cassini*) in "weedy, open country of Middle America and United States"; and *quinquestriata* of "dense deciduous woodland" of northwestern Mexico.

Not considering the South American species detracts somewhat from the zoogeographic analysis. *Aimophila strigiceps* of northern Argentina and Paraguay resembles *A. sumichrasti* in plumage and inhabits brushy fields. *A. stolzmanni* of southwestern Ecuador and northwestern Peru differs from other aimophilas in its large bill, but appears closest to the Haemophila complex in plumage, and like *strigiceps*, inhabits brushy areas. Eliminating these species from possible membership in the other 3 complexes strengthens the zoogeographic conclusions regarding these complexes, while their possible inclusion in the Haemophila complex suggests that the conclusions regarding the evolution and distribution of that group will need expansion and modification.
The 12-inch record, on which songs of all 12 species and "chatters" of 5 are recorded will prove interesting and useful to ornithologists but a headache to librarians. On the whole, the vocalizations on the record well complement those shown on the sonagrams, but cross referencing and editing of the data could be greatly improved. There are no references in the text to the vocalizations on the record, and not all song types on the record are shown in the sonagrams. Nor is there any indication that any sonogram was taken from any song on the disc, although some may have been. Finally, while there are lists of figures and tables in the introductory material, there is no comparable list of the plates showing which vocalizations of which species are represented on each. In the absence of an index, such a list would have been very useful.

This monograph includes a wealth of information on a complex group of finches and is particularly valuable in showing how different kinds of information may be pooled to produce a good understanding of interrelationships within a genus of birds. If comparable studies of such genera as Melozone, Oritur us, Pipilo, and Chondestes are pursued, a better understanding of the relationships among these genera and the complexes within Aimophila will follow.—Robert W. Storer.


GUIDE TO THE YOUNG OF EUROPEAN PRECOCIAL BIRDS. By Jon Fjeldså, illus. by the author. Skrav Nature Publications, Strandgården, DK-3220 Tisvildeleje, Denmark, 1977: 285 pp., 39 color plates, 70 text figs., 1 photo. Danish Kroner 200 (approx. $33).—This is the first guide devoted exclusively to downy young for any part of the globe, and emphasizes 180 species from Europe and Greenland. More than 70 of these species also breed in North America excluding Greenland. In addition to explaining and illustrating characters for identifying downies, the volume includes comments on their ecology and systematics.

Ornithologists have often neglected downies. Collectors often fail to preserve them, and perhaps for this reason, taxonomists have frequently slighted them. As Fjeldså points out, downies in the field are preferably identified by their own features rather than by the adults present as is often done. Where similar species breed in the same locality, identification is particularly challenging. For Europe and Greenland Fjeldså gives characters to identify all precocial downies to species, even for such difficult groups as the gulls, whose downies have often been thought to be indistinguishable. Fjeldså has handled more than 3700 live and preserved downies, an impressive total in view of their scarcity in many collections.

A general account of the biology of precocial birds (pp. 19–23) surveys relationships between nidifugous habits and embryonic maturation of young, nest sites, clutch sizes, adult foraging, and other ecological features. A section on morphology and changes in proportions during growth (pp. 24–30) includes a brief review of taxonomic variations in the structure and appearance of natal plumages. Natal downs exhibit a rachis in only a few avian families including certain ratites, tinamous, some Galliformes, and the Anatidae. As the natal downs of flamingos lack a rachis, the often noted similar appearance of natal plumage in flamingos and swans is superficial. Fjeldså also examines the relationship between habitat and the amount of pattern in downy plumages.

A section on banding downies (pp. 31–34) describes the reshaping of bands to match the cross sectional shape of tarsi. Many chicks too small for banding with conventional
bands that would slip off the leg can be marked by using such bands with a plasticine inner lining that gradually wears away as the leg grows.

A major part of the book contains family and species accounts. English common names follow European rather than American usage with synonyms given for each species in Danish, German, Dutch, and French. In a typical species account Fjeldså describes the downy young in detail, referring to one or more illustrations. Characters for distinguishing similar species are emphasized, and the author notes and illustrates individual variations in downy plumage for especially variable species. Also listed are body length and weight at hatching, time from hatching to flight of young, maximal brood sizes, band size, breeding range in Europe and Greenland, habitat, and time of year at which downies occur. Included are loons, grebes, a flamingo, swans, geese, ducks, grouse, phasianids, a button quail, bustards, rails, a variety of Charadriiformes, and sandgrouse. In accord with Fjeldså’s taxonomic views loons and sandgrouse are placed in the Charadriiformes.

Brief comments on evolutionary relationships are included, and downies of a number of non-European species are illustrated and/or discussed briefly. Certain taxonomic differences in downy patterns are termed “nonadaptive” (p. 12), but would perhaps be better characterized as alternative kinds of adaptation. “Morphocline” phyletic diagrams indicate possible evolutionary affinities within the grebes, Anatidae, grouse, and Charadriiformes, but the evidence supporting these diagrams is not fully presented. In one such diagram eiders are placed in an unconventional arrangement between golden-eyes and mergansers. In the same figure, Fjeldså’s sketch of a downy Anseranas does not agree with the correct description and illustration provided by Delacour (Waterfowl of the World, 4:327 and Plate V. Country Life, London, 1964).

Imperfections of this volume appear minor relative to its considerable merits. Neither a number of spelling errors nor an occasional sentence with peculiar wording detract seriously from the overall presentation. A statement (p. 27) that in certain taxa a plumage of preplumulae is pushed out by a plumage of prepennae needs clarification; it is difficult to visualize how this could occur. Fjeldså uses the term mesoptile but unfortunately does not explain how mesoptile plumages as a category differ from other kinds. Regrettably the text lacks literature citations, though three pages list the consulted publications; a reader wishing to check particular statements could have difficulty finding the sources.

For identifying downy chicks of European precocial species I know of no other book equaling this volume. Many of the author’s illustrations are outstanding, and some may purchase the book for no other reason. The volume is attractively produced, sturdily bound, and fits readily in a field knapsack. It is an appropriate addition to any library with major ornithological holdings, and biologists with special interests in the downy young of any of the families or species considered will want access to it.—GEORGE A. CLARK, JR.


THE COURTSIP OF BIRDS. By Hilda Simon. Dodd, Mead & Co., New York, 1977: 190 pp., 54 color illustrations by the author. $12.95—This book describes the diverse ways that “birds woo and win their mate.” Apparently intended for amateur ornithologists, beginning students of birds and behavior, and nature lovers, it could serve as a good introduction to courtship behavior for any beginning student from junior high school
The text is divided into 5 chapters: Patterns of Courtship Behavior, Plumage Pageantry, Display Acrobatics, Wooing by Work, and Mutual Courtship.

Each chapter begins with a brief poetic description of the courtship of a species typical of the category being discussed. This serves to interest the reader and to introduce the topic. The first chapter describes the general courtship patterns of birds, and provides an introduction for the rest of the text. Simon discusses species recognition, imprinting, social facilitation (not so named), the effect of light, and aerial courtship. The chapter on Plumage Pageantry discusses how birds use feathers in courtship, and includes descriptions of birds of paradise, lyrebirds, and the Great Argus Pheasant. In Display Acrobatics the author describes courtship in grouse, prairie chickens, Ruff, bustard, Ostrich, and manakins. Wooing by Work understandably includes descriptions of bowerbirds, frigate birds, penguins, tits, wrens, and weavers. In the chapter on Mutual Courtship Simon describes Whooping Cranes, swans, geese, ducks, grebes, Jackdaws, and Laughing Gulls. As is obvious from the above list of species, she covers a wide range of species representative of birds in general. As when many non-ornithologists describe avian courtship, she concentrates on the spectacular, showy species whose antics and behavior fascinate the naturalist in all of us. However, sufficient space is not devoted to the majority of species whose monogamous courtship patterns are less spectacular. This treatment will surely give the naive reader an inaccurate picture of the number of species with spectacular courtship patterns. This solitary failing in the book can be forgiven since its intent is to excite interest, and this it does through a lively writing style and delightful illustrations.

Simon's writing is clear and pleasant. She treats such complex behavioral concepts as sexual dimorphism, imprinting, leks, and anthropomorphism well. Her discussion of the role of learning in imprinting, although brief, avoids the usual pitfalls, and she manages to avoid condescension while carefully defining all technical terms. Her writing style is expository, yet poetic. Occasionally her sentences become overly long, sometimes taking an entire paragraph, which may obscure the meaning in some cases.

I found the book to be generally accurate, bearing in mind that the descriptions are brief. However a few points need correction in a future edition. Although a bird may well sing to "encourage his mate" (p. 15), we have no way of knowing this. For a further discussion of such topics readers should refer to D. Griffin's recent book The Question of Animal Awareness. Although ethologists argue about the role of males and females, we still do not refer to males as asserting their dominance, to females as childlike (p. 66), or to a female as seeing the "error of her ways" (p. 128). I know of no ornithologists who "expressed a vague irritation" as they described "the seeming indifference of the peahen when faced" with the splendor of the male's display (p. 70). The role of males displaying on a lek may be socially facilitating as well as for establishing a hierarchy. From my own perspective, the description of Laughing Gull courtship needed editing. I know of no research that indicates that males and females cannot recognize the sex of another Laughing Gull. The charge of a male is to repel intruders, regardless of their sex! The female's appeasement behavior may initiate courtship, but it is not an indication that the male did not perceive her as a female. Additionally, food-begging is not only symbolic in this species, as males do indeed regurgitate food to their mates. Generally, however, the descriptions are accurate, sometimes misleading only because of their brevity.

The color illustrations by the author supplement the descriptions, giving the reader a picture both of the bird and the display or behavior being described. Most illustrations are accurate, although the color on some could be slightly improved. For the non-
taxonomist it would help to identify the species and behavior in the illustrations, although a legend for each illustration does appear at the beginning of the book.

In general, this book is well-written, interesting, fairly accurate, and well-illustrated. I recommend it highly for amateur birders, high-school students, and anyone who enjoys nature. Additionally, it might be very instructive reading some evening for beginning undergraduate ornithology and behavior students.—JOANNA BURGER.


**Manual of Neotropical Birds, Vol. 1.** By Emmet R. Blake. The University of Chicago Press, Chicago and London, 1977: 674 pp., 12 plates (4 in color), 67 wash drawings, numerous range maps. $50.00.—South America has been called the “bird continent,” as the variety of its feathered inhabitants surpasses that of all other tropical land areas of the world. However, a detailed descriptive account of the avifauna in its entirety has never been published. The “Manual” is designed to fill this gap and is the first of a projected series of 4 volumes. The work, once completed, will provide a synthesis of basic data of “all species and subspecies of birds recorded from the mainland of both Central and South America, the continental islands, and adjacent waters” (excluding Mexico, the West Indies, the Galapagos and Falkland Islands). Following the Wetmore sequence, the first volume includes mostly “coastal” and “water birds.” Among the more typically South American families treated are the rheas, tinamous, and cracids (curassows, guans, chachalacas). A brief introductory and general section includes a useful synopsis of families (by K. C. Parkes). The main text provides keys by families for all species to determine the bird “in the hand” and detailed descriptions of species and of all subspecies as recognized by the author. Measurements are given (sample size, range, mean) and the distribution is described and in most cases illustrated by fairly small, yet highly instructive maps. No life history data are summarized, presumably for reasons of space, but references for each species serve as a guide to ecological or more specific “biological” publications. Recent taxonomic sources followed by the author are quoted under the family and under many genus headings. The sequence of species in some families or genera and the generic allocation of certain species differ from those used by de Schauensee in his reference lists of the South American avifauna (*The Species of Birds of South America and their Distribution*, Livingston Publ. Co., Narberth, PA, 1966, and *A Guide to the Birds of South America*, Livingston Publ. Co., Wynnewood, PA, 1970). Of the 600 species treated in Blake’s first volume of the “Manual” just over one third (225 species) are illustrated in full or the head only on 12 plates (4 in color) and in 67 wash drawings scattered through the text. The superb plates are by G. Tudor (except one) who also contributed several excellent text illustrations. The majority of the latter and one plate are by R. V. Keane. Unless the number of plates is increased in future volumes, an inadequate illustrative coverage will be felt especially in the case of the very diverse passerine families.

Blake’s detailed systematic treatment of the Neotropical avifauna, summarizing and updating technical information scattered over a vast literature, will form a sound basis for future field investigators and will stimulate further ornithological studies in South and Central America. For the amateur it will be a dependable source of detailed information on the feathered inhabitants of South America and Central America as far as known today. Hopefully, the remaining volumes will be published without undue delay.
The influence of regional handbooks upon future ornithological research can hardly be overestimated. Therefore, the author of such a work preferably presents the material not only in the form of a summary and compilation of known data but, at the same time, points out unknown aspects of the avifauna at various levels from individual species and species groups to ecological communities. Generally speaking, the Neotropical avifauna is poorly known. New species are still being described at a rate of several per year. The life histories and the behavior of the majority of Neotropical birds have not been studied and little is known on their seasonality and migratory behavior. Relevant publications are listed in the “Manual” at the end of each species account. Nevertheless, I hope brief statements like “Terrestrial forest bird . . .” or “. . . hunts for insect prey in the canopy level . . .” will characterize briefly the ecological stations of species in the diverse Neotropical families to be treated in future volumes. As stated above, the emphasis of the text is on plumage description, measurements and the distribution of all species and their subspecies. The author does not discuss the theoretical basis for his systematic treatment of South American birds and, in future volumes, hopefully will point out more frequently open questions regarding the geographical basis and distribution of species and subspecies. “Subspecies” are often treated as if they were distinct biological entities, their names and text printed in the same large letter type as that used for the species (a smaller letter type for subspecies sections would be helpful in future volumes). Many subspecies are clinally related, grading into each other over wide areas, and their delimitation is highly subjective; or subspecies represent uniform populations in geographic isolation from the main species range; in other instances subspecies or subspecies groups (“megasubspecies”) meet along “hybrid zones.” These and other phenomena of geographic variation and population structure and their relations to environmental factors such as rainfall, seasonality of the climate, the existence of a network of broad rivers, and isolation by mountain ranges need to be brought out for each of the South American bird species (if the available data permit). In view of the differing nature of geographic variation among Neotropical birds, a more flexible treatment of “subspecies” might be considered for future volumes of the “Manual”: e.g., a brief introductory section on general aspects of geographic variation would be useful for species with many “subspecies”; several clinal forms might be discussed jointly as a subspecies group, if necessary helped by tables for measurements, coloration or by maps to illustrate details of distribution (with subspecies names mentioned in the text only). The rigid standard treatment in this volume of species as if they were composed of ± well “defined” subspecies might be considered as typological. To be sure, it is of biological significance to analyze the nature and cause of geographic variation in species populations, but to know the names of subspecies is less important.

Species are also treated in the “Manual” as independent biological entities of equal significance, although many different evolutionary levels are represented, from those species which have barely reached reproductive isolation to distantly related sympatric species. There are numerous South American species which exclude each other geographically in fairly uniform ecological regions presumably as a result of competition. In many but not all of these cases geographical representatives may be combined as allospecies of superspecies. Not a single pair of such parapatric species has been studied along the contact zone to learn how parapaty due to competition (?) “functions” in the field! For this reason it would be useful to map in detail the distribution of species with “peripherally overlapping” or mutually exclusive ranges and to discuss briefly species borders and relationships in an introductory section of each genus where applicable. The useful if small scale maps included at the end of each family section
of the “Manual” depict the distribution of all species. Often several species ranges are combined on a map of all or part of South America as space permitted. It would be useful to indicate in future volumes which of the allopatric or parapatric species could be considered as superspecies or as species groups.

Summarizing, I feel that in the case of avian families with numerous related genera and species the reader of the “Manual” would welcome brief syntheses at various levels which would help visualize the biological significance of certain aspects of geographic variation and distribution or which would point out certain problems of interspecific relations. The linear treatment of species by necessity breaks the avifauna into seemingly “independent” or “isolated” taxonomic units; the author could make an effort to “rebuild” the fauna, at least partially, by including brief sections on systematic, ecological or distributional aspects at the level of species, genera, and/or families. Hopefully, the author also plans for a future volume a section reviewing such general topics as the regionally varying systematic composition of forest and nonforest avifaunas, resident versus migrant species, annual cycles among Neotropical birds, and historical aspects of the differentiation of the South American avifauna.

In concluding I list a few comments concerning certain details of the text and the maps. In coastal and montane species it might be advisable to indicate the range by a heavy line or a series of dots following the coast line or a mountain slope, respectively, to emphasize the linear extension of their ranges. A few minor corrections may be listed; p. 29, key under C. strigulosus (♀), . . . south of the Amazon. The statement of “many sightings of the Red-head (A. americana) in Costa Rica and central Panama” (p. 250) is based on a misunderstanding and does not refer to this species (E. Eisenmann, pers. comm.). Daptrius americanus (p. 357, top) is distributed in Brazil south to (not of) Mato Grosso and São Paulo. Dr. J. O’Neill recently rediscovered Penelope albipennis (p. 412) in northwestern Peru. Rhynchortyx cinctus (p. 453) ranges eastward in northern Colombia to the Magdalena Valley (Volador; Westmore, Smiths. Misc. Coll. 150, pt. 1:332). Haffer (Publ. Nuttall Ornithol. Club 14:106, 1974) considers the form ochroptera as a subspecies of Psophia crepitans rather than of P. leucoptera. Laterallus exilis has also been collected in Amazonian Ecuador (Limoncocha; Pearson, Condor 77: 97, 1975; this locality is not located in eastern Peru). Typographical errors are rare.

Judging by this first volume, Blake’s “Manual” promises to become the basic descriptive of Neotropical birds for many years to come, indispensible for professional and amateur ornithologists alike.—JÜRGEN HAFFER.
The Wilson Bulletin

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*See Ornithological News, p. 308, for address for ms submission.
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AUTUMN BIRD CASUALTIES AT A NORTHWEST FLORIDA TV TOWER: 1973–1975

ROBERT L. CRAWFORD

Accounts of nocturnal accidents to migrating birds at tall, lighted structures are numerous (Nisbet 1970) but most represent species listings covering 1 or 2 night kills. Tordoff and Mengel (1956), Goodpasture (1963a,b), and Taylor (1972, 1973) showed that more detailed analyses of tower kills contribute much to our understanding of many aspects of avian migration, particularly to the differential migration of age and sex classes. Even so, Johnson’s (1973) statement “... the temporal and geographic complexities of migration ... are only beginning to be understood” probably applies to most migratory species. Many more data from different sites are needed. This paper presents age and sex data for 3223 birds killed at the WCTV tower in northwest Florida during the autumns (August–November) of 1973–1975. Comparisons with other studies, particularly to the one by Taylor and Anderson (1973) in central peninsular Florida are made.

METHODS

Stoddard (1962), Stoddard and Norris (1967), and Crawford (1974) gave the species, numbers, and seasonal variation of birds killed at the WCTV tower on Tall Timbers Research Station, Leon County, Florida, and complete descriptions of the 308 m tower and its 14 ha cleared site. In 1973, the grounds were checked for dead birds daily at 07:30 and the control of predators that eat the dead birds was essentially limited to experiments (Crawford 1971, 1974). In 1974 and 1975, the tower grounds were checked at daybreak and a more rigorous program of predator control was instituted that included both trapping and poisoning. In all years the birds were frozen soon after collection and within 3 months of death were thawed and dissected to determine the age and sex by examination of the skull and gonads (Miller 1946, Goodpasture 1963b). I kept notes on plumage abnormalities, stomach contents, molt, and other physical aspects of most of the specimens.

RESULTS

Numbers and species recorded during the study.—In the autumn of 1973, 261 individuals of 57 species were collected. For the same period in 1974,
1832 individuals of 87 species, and in 1975, 1771 individuals of 90 species were found. The total for the 3 autumns was 3864 individuals of 109 species. The disparity between the number of birds recorded in 1973 and subsequent years is due primarily to the reintroduction of predator control at the tower. Compared to 3 predators removed in 1973, 42 were removed from the tower grounds in 1974–1975 and there was evidence that 28 others were eliminated. Most of those handled were Virginia opossums (Didelphis virginiana), feral domestic cats (Felis catus), and Great Horned Owls (Bubo virginianus).

On 6 nights during the study period, more than 100 dead birds were recorded: 17 October 1973 (133), 5 September 1974 (134), 23 September 1974 (220), 17 October 1974 (971), 14 September 1975 (636), and 15 September 1975 (486). These are 66.7% of the grand total and all were associated with the onset and passage of cold fronts.

Physical aspects of the tower casualties.—Plumage abnormalities were rare. Partial albinism was observed in an adult ♀ Yellow-rumped Warbler (Dendroica coronata) and an unsexed adult Field Sparrow (Spizella pusilla). An adult ♀ Bay-breasted Warbler (Dendroica castanea) with an abnormally pale-yellow head appeared to be partially xanthocroistic (Tall Timbers Res. Sta. #3267). Molting individuals were also rare but nearly one-half of the Gray Catbirds (Dumetella carolinensis) examined, including all age and sex classes, were in body molt. One immature ♀ Ovenbird (Seiurus aurocapillus) had sheathed rectrices when found on 15 September 1975.

I examined the stomachs of all the birds from 1973 and those found from August–September of 1974 and found virtually all to be empty. Other workers have recorded similar results for migrating birds (Tordoff and Mengel 1956:8). I did find, however, that Yellow-billed Cuckoos (Coccyzus americanus) and Black-billed Cuckoos (C. erythropthalmus) consistently had full stomachs.

Sex and age ratios.—Sex and age data from the WCTV tower samples are in Table 1 and the species included are only those with large sample sizes (usually ≥10). The total male:female ratio is virtually 1:1 (50.2% ♂ ♂) and the 46.2% adult proportion is essentially what others have found for adult survival rates (Ricklefs 1973:404). Individual species often do not have these expected ratios and this may be due to real inequalities within the populations, year-to-year variation, or to differential migration by age or sex classes.

Murray (1966) defined 3 types of differential migration: non-overlapping asynchronous in which all individuals of one age or sex class precede the others (or vice versa); overlapping asynchronous in which the timing of the age and sex classes overlap, but one peaks before the others; and
**Table 1**

**SEX AND AGE RATIOS OF BIRDS KILLED AT THE WCTV TOWER: AUTUMNS 1973–1975**

<table>
<thead>
<tr>
<th>Species</th>
<th>Total examined</th>
<th>Ad:Im</th>
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<th>A♂♂:1♀♀</th>
<th>A♀♀:1♂♂</th>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Indigo Bunting</td>
<td>47</td>
<td>29:18</td>
<td>23:18</td>
<td>17:6</td>
<td>11:6</td>
<td></td>
</tr>
<tr>
<td><em>Passerina cyanea</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Savannah Sparrow</td>
<td>21</td>
<td>6:15</td>
<td>9:9</td>
<td>2:7</td>
<td>3:6</td>
<td></td>
</tr>
<tr>
<td><em>Passerculus sandwichensis</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grasshopper Sparrow</td>
<td>7</td>
<td>3:4</td>
<td>3:2</td>
<td>1:2</td>
<td>2:0</td>
<td></td>
</tr>
<tr>
<td><em>Ammodramus savannarum</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other species</td>
<td>177</td>
<td>79:89</td>
<td>74:80</td>
<td>32:35</td>
<td>41:35</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>3223</td>
<td>1455:169</td>
<td>1278:1267</td>
<td>617:629</td>
<td>672:546</td>
<td></td>
</tr>
</tbody>
</table>

1Italicized ratios are significantly at variance from equality (P < .05 by χ²).
2Dated entries are from single night kills.

synchronous in which the timing and numbers of the sex and age classes are the same. Differential migration behavior may be temporal, geographical, or both (King et al. 1965).

Seven species exhibited evidence of temporal differential migration at the WCTV tower (Table 2) and all cases involved age classes only. The significance (at the P < .05 level) was determined by the variance test for homogeneity of the binomial distribution (Snedecor and Cochran 1967:240). For the Red-eyed Vireo, Tennessee Warbler, and Ovenbird there was an early peak by the adults, and for the Gray Catbird, Wood Thrush, Black-and-white Warbler, and Common Yellowthroat the immatures peaked early. All represent an overlapping asynchronous migration pattern.

Taylor and Anderson (1973) studied autumn bird casualties at the
Table 2
SEASONAL VARIATION IN AGE CLASSES AT THE WCTV TOWER, AUTUMNS 1973-1975

<table>
<thead>
<tr>
<th>Species</th>
<th>August 16-31</th>
<th>September 1-15</th>
<th>September 16-30</th>
<th>October 1-15</th>
<th>October 16-31</th>
<th>November 1-15</th>
</tr>
</thead>
<tbody>
<tr>
<td>* Gray Catbird</td>
<td>0:0</td>
<td>0:5</td>
<td>9:14</td>
<td>18:15</td>
<td>12:15</td>
<td>0:0</td>
</tr>
<tr>
<td>* Wood Thrush</td>
<td>0:0</td>
<td>0:0</td>
<td>0:4</td>
<td>2:3</td>
<td>7:10</td>
<td>0:0</td>
</tr>
<tr>
<td>** Black-and-white Warbler</td>
<td>1:2</td>
<td>9:39</td>
<td>2:3</td>
<td>4:1</td>
<td>13:14</td>
<td>0:0</td>
</tr>
<tr>
<td>* Tennessee Warbler</td>
<td>0:0</td>
<td>0:0</td>
<td>2:2</td>
<td>3:5</td>
<td>7:34</td>
<td>0:3</td>
</tr>
<tr>
<td>** Ovenbird</td>
<td>0:0</td>
<td>35:53</td>
<td>2:9</td>
<td>6:4</td>
<td>19:89</td>
<td>1:2</td>
</tr>
<tr>
<td>** Common Yellowthroat</td>
<td>0:0</td>
<td>4:42</td>
<td>11:31</td>
<td>17:17</td>
<td>14:20</td>
<td>1:2</td>
</tr>
<tr>
<td>Red-eyed Vireo</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>** Ad♂♂:Im♂♂</td>
<td>1:3</td>
<td>146:98</td>
<td>33:30</td>
<td>3:26</td>
<td>0:30</td>
<td>0:0</td>
</tr>
<tr>
<td>** Ad♀♀:Im♀♀</td>
<td>0:2</td>
<td>170:72</td>
<td>60:14</td>
<td>6:11</td>
<td>8:14</td>
<td>0:0</td>
</tr>
<tr>
<td>** Ad?:Im?</td>
<td>0:0</td>
<td>15:68</td>
<td>9:25</td>
<td>0:0</td>
<td>1:51</td>
<td>0:0</td>
</tr>
<tr>
<td>** Ad:Im</td>
<td>1:5</td>
<td>331:238</td>
<td>102:69</td>
<td>9:37</td>
<td>9:95</td>
<td>0:0</td>
</tr>
</tbody>
</table>

1 Unless otherwise noted, numbers are adults:immatures.
* Not significant (P > .05).
** Significant (P < .05).

WDBO tower in Orange County (central peninsular), Florida for the years 1969–1971, and their data seem an appropriate comparison with those from the WCTV tower for determining evidence of geographic variation in differential migration. Table 3 compares those species from WCTV and WDBO which had age or sex ratios significantly different from equality by simple chi-square tests. Intertower comparisons were based on the arcsin test for the equality of 2 percentages (Sokal and Rohlf 1969:608). The species in Table 3 are of 2 classes: (1) those that have age or sex classes significantly at variance from equality the same way at both towers, and (2) those that show a difference in ratios between the towers. The Acadian Flycatcher is an exception that fits neither class. Of those species in the first class, the Swainson’s Thrush, Tennessee Warbler, and Blackburnian Warbler show a preponderance of immature birds at both towers, while the Veery, White-eyed Vireo, Swainson’s Warbler, Northern Parula, Palm Warbler, and Bobolink show a preponderance of adults at both sites. The Bay-breasted Warbler and the Ruby-crowned Kinglet had high percentages of females, while the Northern Parula had a preponderance of males. The species making up the second class had different age ratios at the 2 towers and all but the Red-eyed Vireo and the Yellow-rumped Warbler had a higher percentage of immature birds at the WCTV tower. The exceptional species (Acadian Flycatcher) had a preponderance of adults at the WCTV tower but none of this species was recorded at the WDBO site.
### Table 3

**Species Showing Significant Differences from Equality in Age or Sex Classes at the WCTV Tower (This Study) and at the WDBO Tower (Taylor and Anderson 1973)**

<table>
<thead>
<tr>
<th>Species</th>
<th>Adults:Imm.'s</th>
<th>Sexes:</th>
<th>WCTV</th>
<th>WDBO</th>
<th>WCTV</th>
<th>WDBO</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>**</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acadian Flycatcher</td>
<td>12:4</td>
<td>0:0</td>
<td>4:10</td>
<td>0:0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Short-billed Marsh Wren</td>
<td>1:19</td>
<td>**</td>
<td>24:21</td>
<td>4:9</td>
<td>15:25</td>
<td></td>
</tr>
<tr>
<td>Gray Catbird</td>
<td>39:50</td>
<td>**</td>
<td>100:41</td>
<td>48:34</td>
<td>60:70</td>
<td></td>
</tr>
<tr>
<td>Swainson’s Thrush</td>
<td>20:56</td>
<td>3:11</td>
<td>42:15</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ruby-crowned Kinglet</td>
<td>—:—</td>
<td>—:—</td>
<td>9:24</td>
<td>9:31</td>
<td></td>
<td></td>
</tr>
<tr>
<td>White-eyed Vireo</td>
<td>17:7</td>
<td>41:17</td>
<td>11:12</td>
<td>25:33</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yellow-throated Vireo</td>
<td>0:10</td>
<td>**</td>
<td>3:0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red-eyed Vireo</td>
<td>452:444</td>
<td>**</td>
<td>15:76</td>
<td>370:357</td>
<td>43:33</td>
<td></td>
</tr>
<tr>
<td>Black-and-white Warbler</td>
<td>29:59</td>
<td>**</td>
<td>60:48</td>
<td>44:32</td>
<td>47:61</td>
<td></td>
</tr>
<tr>
<td>Swainson’s Warbler</td>
<td>7:1</td>
<td>19:8</td>
<td>4:4</td>
<td>11:16</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Worm-eating Warbler</td>
<td>7:19</td>
<td>**</td>
<td>20:5</td>
<td>5:15</td>
<td>15:10</td>
<td></td>
</tr>
<tr>
<td>Tennessee Warbler</td>
<td>12:44</td>
<td>6:8</td>
<td>21:20</td>
<td>8:6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern Parula</td>
<td>54:29</td>
<td>211:114</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yellow Warbler</td>
<td>4:14</td>
<td>**</td>
<td>8:2</td>
<td>8:5</td>
<td>5:5</td>
<td></td>
</tr>
<tr>
<td>Yellow-rumped Warbler</td>
<td>30:24</td>
<td>**</td>
<td>42:11</td>
<td>18:22</td>
<td>11:26</td>
<td></td>
</tr>
<tr>
<td>Blackburnian Warbler</td>
<td>23:75</td>
<td>3:10</td>
<td>29:32</td>
<td>8:5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bay-breasted Warbler</td>
<td>69:35</td>
<td>6:7</td>
<td>26:50</td>
<td>3:10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palm Warbler</td>
<td>53:19</td>
<td>305:175</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern Waterthrush</td>
<td>21:34</td>
<td>**</td>
<td>84:45</td>
<td>22:23</td>
<td>51:78</td>
<td></td>
</tr>
<tr>
<td>Bobolink</td>
<td>26:5</td>
<td>111:23</td>
<td>12:12</td>
<td>68:63</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Savannah Sparrow</td>
<td>6:15</td>
<td>**</td>
<td>20:8</td>
<td>9:9</td>
<td>11:15</td>
<td></td>
</tr>
</tbody>
</table>

1 Ratios in italics are significantly at variance from equality \( (P < 0.05 \) by \( \chi^2 \)).

2 Asterisks between ratios indicate significantly different \( (P < 0.05) \) percentages of either adults or males (see text).

### Discussion

The different age and sex ratios revealed in this study may be due to differential migration, variance within the populations, or year-to-year variation. Some age and sex data from birds killed at the WCTV tower in previous years are available in appropriate form for comparison with the results of the present study. Gifford and Odum (1965) found 102 of 186 Bobolinks to be males, a ratio that is statistically insignificant, and D. W. Johnston (pers. comm.) examined 32 Bobolinks from September 1966 and found them all...
to be adults evenly divided for sex. These results are essentially what I found for that species. Johnston and Downer (1968) and Johnston (1970) examined Indigo Buntings killed in the 1960's and found, as I did, slightly more adults than immatures, but consistently there were more females than males. I found slightly more males (23) than females (18) but neither my ratios nor those of Johnston are significant. Nolan and Mumford (1965) examined 286 Prairie Warblers killed in the late 1950's and early 1960's and found 73% to be adults and 50.3% to be males; my figures are 75% and 50%, respectively. W. K. Taylor (pers. comm.) examined 183 Common Yellowthroats killed between 1960 and 1967 and found 50 (26.6%) to be adults which is virtually the same as the 29.4% reported here. Thus species for which WCTV data are available from earlier years show essentially the same age and sex ratios found in this study.

The data in Table 2 generally agree with the literature on these species. Tordoff and Mengel (1956), Goodpasture (1963a,b), Murray (1966), and Taylor and Anderson (1973) all recorded an early peak of adults for the Red-eyed Vireo. The age ratio, however, for this species killed at WCTV on 5 September 1974 (Table 1) has a high percentage of immatures on an early date which indicates there may be some yearly variation in the basic pattern. Tordoff and Mengel (1956) indicated that Gray Catbirds showed an overlapping asynchronous pattern with the adults peaking first, but this was based on a sample from one night. My data for this species seem to agree more closely with those of Barry (1971), for in both cases the adult peak occurred well after the immatures had begun an apparently peakless migration. Tordoff and Mengel (1956) also indicated that in Common Yellowthroats the adults peaked first, while Barry (1971) found a synchronous pattern for this species. W. K. Taylor (pers. comm.) found that in peninsular Florida, the immatures of this species probably peak first which is also the case at the WCTV tower. Goodpasture (1963b) noted an early peak in immature Black-and-white Warblers and an early peak in adult Tennessee Warblers. Taylor (1972) indicated an early peak by adult Ovenbirds. The remaining species (i.e., those not in Table 2) show apparently synchronous patterns but in many cases the sample sizes are too small to allow decisions one way or the other.

Some of the data in Table 3 may well indicate cases of differential migration, but for some of the species other factors may be affecting the results. One bias that tower kills share is that they are dependent on severe weather for large kills. Since the frequency and severity of cold fronts that usually cause such weather in autumn increase from August through October, those species (or age and sex classes) that migrate very early will be absent or poorly represented (Nolan and Mumford 1965). Thus, such relatively
common nocturnal migrants as the Louisiana Waterthrush (*Seiurus motacilla*) and Orchard Oriole (*Icterus spurius*), both of which are early migrants, are poorly represented at both the WCTV and WDBO towers. Similarly, there is only one record of an early migrating adult of the “Traill’s Flycatcher” complex (*Empidonax traillii* and *E. alnorum*) at WCTV (Crawford 1976). An early and relatively unsampled age or sex class might account for some of the unequal ratios found at either WCTV, WDBO, or both. Species that might fall into this category are the Northern Parula (with a high percentage of males at both towers) and the Veery, White-eyed Vireo, Swainson’s Warbler, Northern Parula, and Bobolink (all with a preponderance of adults at both towers). However, this seems an unlikely explanation for the preponderance of adults in the Palm Warbler or the larger number of females in the Bay-breasted Warbler, since both species are rather late migrants. The high percentage of females for the Ruby-crowned Kinglet at both sites is probably due to sexual displacement geographically on the wintering grounds with the males occupying the northernmost part of the winter range (S. A. Gauthreaux, Jr., pers. comm.). This behavior would confer a selective advantage for early arrival of the males on the breeding grounds in the spring to secure choice territories: it would also serve to reduce intersexual competition during the rigorous winter months (Selander 1966). Since in the eastern portion of its range the kinglet winters entirely within the United States, individuals killed at WCTV and WDBO would mostly be the more southerly wintering females.

Fourteen species in Table 3 had different age ratios at the 2 towers and all but the Red-eyed Vireo and the Yellow-rumped Warbler had a preponderance of immatures at WCTV. The relatively high number of adult Red-eyed Vireos at WCTV is most likely a result of the 2 large kills on 14 and 15 September 1975 (Table 1) which is early in the season when normally there are more adults aloft than immatures (references cited earlier). For the remaining 12 species, the evidence suggests that the adults and immatures follow largely different migration routes in the southeastern United States. The 2 towers are sampling different migration systems: the birds killed at WCTV in autumn are primarily trans-Gulf migrants, i.e., most make a non-stop flight across the Gulf of Mexico to Central America (Odum 1960) whereas those killed at WDBO are primarily circum-Gulf migrants, i.e., most fly from the Atlantic coast to South America or island-hop through the West Indies after leaving the Florida peninsula (Taylor 1973). Allopatry of age classes on the wintering grounds, a well known phenomenon (Lack 1954:245, King et al. 1965), would account for the significantly different ratios found at the 2 towers, for as the birds move south, the age classes
would tend to segregate into the different migration systems to reach their separate wintering areas.

SUMMARY

Ages and sexes were determined for 3223 birds killed at the 308 m WCTV tower in northwestern (Leon County) Florida in the autumns of 1973–1975. The data are compared with those from other studies, especially one at a tower in central peninsular Florida. The $\delta : \Omega$ ratio at WCTV was 1278:1267 (50.2% $\delta$) and the adult:immature ratio was 1455:1694 (46.2% adult). Seven species showed differential migration of age and sex classes temporally at the WCTV tower. For 12 species, the trans-Gulf migrants killed at WCTV had significantly more immatures than did the circum-Gulf migrants killed in peninsular Florida. The peninsular migrants had significantly high ratios of adults when compared with those from WCTV. It is suggested that adults and immatures of some species follow largely different migration routes as a result of allopatry on the wintering grounds.

ACKNOWLEDGMENTS

Data from ca. 220 birds came from G. T. Austin, D. W. Johnston, R. L. Marsh, and W. K. Taylor, who received the specimens for other studies. James Atkinson, W. W. Baker, Clifford Sloan, and J. H. Wiese have helped in picking up the birds at WCTV. David Peterson provided advice on trapping techniques. Baker, Taylor, D. B. Means, and H. M. Stevenson made helpful comments on earlier drafts of the paper. N. O. Wamer provided a great deal of help and encouragement in all phases of the study.

LITERATURE CITED

Crawford • FLORIDA TOWER KILLS


TALL TIMBERS RESEARCH STATION, RT. 1, BOX 160, TALLAHASSEE, FL 32312.

ACCEPTED 6 APR. 1977.
WHITE PELICAN PRODUCTION AND SURVIVAL OF YOUNG AT CHASE LAKE NATIONAL WILDLIFE REFUGE, NORTH DAKOTA

ROBERT F. JOHNSON, JR. AND NORMAN F. SLOAN

The current status of the White Pelican (Pelecanus erythrorhynchos) in North America is unclear. Two recent surveys have been conducted (Lies and Behle 1966, Sloan 1973) and each have placed the continental population at between 30,000 and 35,000 individuals. This pelican has been placed on the blue list of bird species that should be closely watched because unexplained population declines have occurred throughout its range (Arbib 1975).

Many authors, including Hall (1925), Low et al. (1950), Schaller (1964), and Kolstoe (1966) have reported on the nest success and pre-fledging survival of the White Pelican. In 1973, we undertook a study at Chase Lake National Wildlife Refuge in North Dakota on some aspects of the biology of White Pelicans. Here we report our results relating to nest success and pre-fledging survival and relate these results to the distances adults seem to have to travel to feed.

STUDY AREA AND METHODS

Chase Lake National Wildlife Refuge is located approximately 13 km north of Crystal Springs in Stutsman County, North Dakota. The surface of the 1775 ha area is covered by approximately 50% water, 45% native and tame grasses, and the remainder marsh and brush. The refuge is typical of the Coteau region of the Missouri plateau (U.S.D.I. 1971).

Chase Lake is highly alkaline and supports no fish population. Two islands, totaling 6.48 ha in size, lie within the lake. The large island is located .4 km from shore while the smaller island is .2 km from the mainland. Both islands grade gradually from the shore to central areas which are located 3 m above lake level on the small island and 5 m above lake level on the large island.

The dominant plant species found on the islands include annual marsh elder (Iva xanthifolia), which forms dense stands over much of the islands, wild barley (Hordeum jubatum), and various sedges (Carex spp.) which grow along the shoreline. Lamb’s quarters (Chenopodium album) and the narrow-leaved goosefoot (Chenopodium leptophyllum) grow in association with the marsh elder.

The Chase Lake colony is the largest breeding concentration of White Pelicans in North America, varying from 4000 to 5000 breeding pairs annually (Sloan 1973). During the periods 25 June through 28 July 1973 and 24 April through 10 June 1974, Johnson observed synchronized breeding colonies daily from a blind.

Number and fate of nests, number and fate of young and their behavior, including sibling rivalry, adult aggression, and feeding activity of the young, were recorded. Behavioral patterns were observed with the aid of a 20 x 60X spotting scope.

In 1974, 100 young, less than 3 days old, were marked with self-piercing, size 1 web tags (Style 4-1005, National Band and Tag Company, 721 York St. Newport, Kentucky 346-352...
Reported during age 41072). Tags were placed on young in 40 nests containing 2 young each and on young in 21 nests containing a single bird. In 1975, 176 young in nests with 2 birds each and less than 3 days old were marked with web tags.

Nest checks were conducted on a weekly basis until the young reached 3 weeks of age and were no longer easily approachable. Surveys were maintained at 1 week intervals in order to keep disturbance to a minimum.

Frequent searches were made for spaghetti-type fish tags on the breeding islands. The nesting colonies were searched by slowly walking through them and carefully observing the ground. The colored fish tags contrasted with the ground litter in the colonies which aided in their recovery. Such tags are used to mark fish in order to study their movements, longevity, etc. They pass through the digestive tract of pelicans and can provide an indication of pelican foraging areas.

RESULTS AND DISCUSSION

Foraging.—The diet of the White Pelican consists primarily of rough fish and amphibians (Mansell 1965). Food requirements for the Chase Lake colony, based on 8000 breeding adults, are substantial (Table 1). As Chase Lake supports no fish life, the pelicans must find food elsewhere. Reported round-trip foraging distances for White Pelicans range from 96 km (Behle 1958) to 241.5 km (Low et al. 1950). At Chase Lake round-trip distances have ranged up to 611 km (Fig. 1). Foraging distances have been based on the recovery of 31 fish tags which were found on the breeding islands in 1974. These tags had been placed on walleyes (Stizostedion vitreum) and northern pike (Esox lucius) by personnel of the North Dakota Game and Fish Department. One tag was placed on a bigmouth buffalo (Ictiobus cyprinellus) by personnel of the U.S. Fish and Wildlife Service when the fish was released in Lake Oahe in South Dakota. Twenty-eight of the recoveries were within a 128 km radius of Chase Lake, however, the 3 tags that were recovered from greater distances indicate that foraging movements may be significantly greater than 241.5 km round-trip. The bulk of the pelican diet consists of rough fish and amphibians and presently we have no means to determine where this food is obtained.

Nest abandonment.—Both members of the pelican pair participate in incubation, one relieving the other after a period of foraging. Nest abandonment may result when one adult is not relieved after a prolonged absence of the mate. Knopf (1976) reported that each adult was present on the nest for 72 h (N = 14) during the incubation period. Nest relief occurred every 24 (N = 18) or 48 (N = 2) h after the eggs had hatched. The adults in the colonies that we observed were not marked and we were unable to distinguish between individuals on the basis of facial patterns. Consequently, we have insufficient data to determine a nest relief time sequence for Chase Lake.

During the observation of the synchronized breeding colony in 1974, 6
Table 1

Estimated Food Requirements of the Chase Lake Pelican Flock Based on a 108 Day Breeding Season

<table>
<thead>
<tr>
<th></th>
<th>Consumption¹</th>
<th>Number</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td>1.8 kg per day per adult</td>
<td>8000</td>
<td>1,567,607 kg</td>
</tr>
<tr>
<td>Young</td>
<td>68 kg to flight stage</td>
<td>4320²</td>
<td>293,926 kg</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>1,861,533 kg</td>
</tr>
</tbody>
</table>

¹ Consumption rate reported by Hall (1925).
² Number based on a fledging rate of 1.08 young per nest to maintain colony at 8000 breeding adults (Strait and Sloan 1974).

of 18 abandoned nests were deserted without any apparent reason. The incubating birds flew off the nest and left the area. No other birds showed any signs of disturbance. These nests were abandoned at least 2 weeks after our observation blind had been erected. The observer was not visible to the colony while entering the blind, thus making it highly unlikely that human disturbance was the cause of abandonment. In addition, an adult was observed throwing both of its less than 5-day-old young from the nest. Two

Fig. 1. Localities where tagged fish were released whose tags later showed up in the Chase Lake White Pelican colony. Circled numbers indicate the number of tags recovered from that locality.
other small young were seen in the air, although the adult was not actually seen throwing these young from the nest. Both instances occurred in the colony under observation. The synchronized colony that was observed in 1973 contained 26 nests with 3 nests abandoned (31% nest loss) and the 1974 colony was comprised of 21 nests with 18 abandoned (75% nest loss). Ninety-nine% of 219 nests in 4 additional colonies were abandoned in 1974. These colonies were visited only once during the nesting sequence. Nest abandonment was a serious problem in other colonies, although, in order to minimize disturbance, we did not closely observe additional colonies.

Brown and Urban (1969) observed both eggs and young abandoned by the Great White Pelican (*Pelecanus onocrotalus*) at Lakes Natron and Rukwa in Tanzania when food was no longer available. Feeley (1962) noted a complete lack of breeding in years of inadequate food supplies at Lake St. Lucia in Zululand.

High rates of nest abandonment in 1974 may be attributed to difficulty in obtaining food. The birds may have been forced to travel further in response to low water levels and spend more time foraging. Incubation periods increased and nest relief did not occur, causing the incubating birds to abandon their nests. Knopf (1976) observed 22.4% of 1930 nests abandoned at Gunnison Island in Great Salt Lake, Utah, in 1973 and 23.7% of 2348 nests in 1974. The extremely high rates of nest abandonment and aberrant adult behavior observed in 1974 might be attributable to some external factor, such as a difficulty in obtaining food.

**Survival.**—Survival at time of nest departure in the observed colonies was .62 young per nest in 1973 and .21 young per nest in 1974. Young left the nest at between 2 and 3 weeks of age. In 1973, 16 young left the observed colony, while in 1974, 5 young departed from the nests. Overall colony production (fledged young) was estimated at 2100 young from 3911 nests in 1973 (.54 young per nest). In 1974 an estimated 1200 young were produced from 3082 nests (.39 young per nest).

In both 1974 and 1975, the survival of the larger nestlings in nests with 2 young until 1 and 2 weeks after hatching was significantly greater than that of the smaller birds ($\chi^2 = 25.96, p < .01$ in 1974; $\chi^2 = 66.32, p < .01$ in 1975). At least 1 week after hatching in 1974, 79.5% of the large young and 10.3% of the small young in 2-bird nests ($N = 40$) were known to be alive. In 1975, 74% of the large young and 23% of the small young in 2-bird nests ($N = 38$) were known to be alive at least 1 week after hatching (Table 2). All of the young in nests with single birds ($N = 21$) were alive 2 weeks after hatching in 1974.

In over 90% of the observed nests, the smaller nestling died as a direct result of physical abuse by the older young. The larger nestling was ob-
Survival of Web-tagged Young from 2-Chick Nests at Chase Lake in 1974 and 1975

<table>
<thead>
<tr>
<th>Size of Young</th>
<th>Year</th>
<th>Number tagged</th>
<th>Number alive to 1 week</th>
<th>Number alive to 2 weeks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large</td>
<td>1974</td>
<td>39</td>
<td>31</td>
<td>23</td>
</tr>
<tr>
<td>Small</td>
<td>1974</td>
<td>39</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Large</td>
<td>1975</td>
<td>25</td>
<td>21</td>
<td>16</td>
</tr>
<tr>
<td>Small</td>
<td>1975</td>
<td>25</td>
<td>13</td>
<td>2</td>
</tr>
<tr>
<td>Large</td>
<td>1975</td>
<td>25</td>
<td>16</td>
<td>-</td>
</tr>
<tr>
<td>Small</td>
<td>1975</td>
<td>25</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Large</td>
<td>1975</td>
<td>38</td>
<td>-</td>
<td>23</td>
</tr>
<tr>
<td>Small</td>
<td>1975</td>
<td>38</td>
<td>-</td>
<td>1</td>
</tr>
</tbody>
</table>

served continually pecking and biting the small young. The adult male made no active effort to terminate the harassment. Adults did end the abuse passively by separating young during brooding.

Some smaller nestlings probably died of starvation. In these cases the larger young prevented the smaller from feeding as frequently or successfully as itself. In 1974, 187 feeding attempts were observed in the colony under observation. Large young initiated 122 (65.2%) of these attempts. Fifty-one successful feeding attempts were observed with large young getting the food in 38 (74.5%) of them.

The intense sibling rivalry as well as the high rates of nest abandonment observed at Chase Lake may be the result of difficulty in obtaining food. Some nest abandonment was likely caused by investigative activities; however, it is highly unlikely that entire colonies could be abandoned after only 1 visit by a single researcher.

There is significant discrepancy in the production figures among North American White Pelican colonies (Table 3). Most reported high survival rates are associated with quick visual observations, while low survival rates were found when actual counts of nests and young were made. Very few data dealing with the survival rates of juvenile White Pelicans from hatching exist. Consequently, any attempts to explain low production in terms of environmental factors results in a lack of supporting data from other colonies. A more comprehensive system of monitoring all White Pelican colonies is necessary if we are to determine if factors such as nest abandonment and sibling rivalry are, in fact, related to food availability or are a normal segment of the reproductive process in the White Pelican.

Previous studies have shown that sibling rivalry may be related to factors other than food. Ingram (1959) found that in many species of birds of prey
TABLE 3
PRODUCTION OF SELECTED WHITE PELICAN COLONIES IN NORTH AMERICA

<table>
<thead>
<tr>
<th>Location</th>
<th>Number of Nests</th>
<th>Number of Young</th>
<th>Young per Nest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellowstone Lake Wy. (Schaller 1964)</td>
<td>298</td>
<td>117</td>
<td>.39</td>
</tr>
<tr>
<td>Lake of the Woods Ont. (Mansell 1965)</td>
<td>160</td>
<td>61</td>
<td>.38</td>
</tr>
<tr>
<td>East Shoal Lake Man. (Hosford 1955)</td>
<td>282</td>
<td>92</td>
<td>.33</td>
</tr>
<tr>
<td>Chase Lake N.D. (1974)</td>
<td>24</td>
<td>5</td>
<td>.21</td>
</tr>
<tr>
<td>LaCreek NWR S.D.¹</td>
<td>900</td>
<td>1100</td>
<td>1.22</td>
</tr>
<tr>
<td>Medicine Lake NWR Mt.²</td>
<td>1700</td>
<td>1850</td>
<td>1.23</td>
</tr>
<tr>
<td>Anaho Island NWR Nev.³</td>
<td>3000</td>
<td>2980</td>
<td>.99</td>
</tr>
<tr>
<td>Bowdoin NWR Mt.³</td>
<td>1250</td>
<td>1480</td>
<td>1.18</td>
</tr>
</tbody>
</table>

¹Figures are for 1971 (Sloan 1973).

the smallest young was eliminated regardless of the amount of food available. Gannets (Morus bassana) are capable of raising and feeding 2 young even though the second hatched young is virtually always killed by the first (Nelson 1964). Only the first hatched young of Sandhill Cranes (Grus canadensis) and Whooping Cranes (Grus americana) fledge, since the second is eliminated by the extreme aggressiveness of the older young (Miller 1973). However, the possibility of other factors influencing the survival of the younger sibling should not be completely discounted at present.

SUMMARY

Foraging distances for the Chase Lake flock range up to 611.8 km round-trip or twice as far as previously reported. Nest abandonment accounted for 31% of the nest loss in 1973 and 75% in 1974 in intensely observed colonies. It also appeared to be a significant problem throughout the entire colony in both years. The larger nestling in 2-chick broods survived more frequently than the smaller one in both 1974 and 1975. One week after tagging in 1974, 79.5% of the large young and 10.3% of the small young in 2-bird nests (N = 40) were known to be alive. In 1975, 74% of the large young and 28% of the small young in 2-bird nests (N = 88) were alive 1 week after tagging. Survival of small young in 2-bird nests was less than 5% after 2 weeks.

Large young fed more frequently and successfully than small young in 2-bird nests. In 1974, 187 feeding attempts were observed. The larger young initiated 122 (65.2%) of these attempts. Fifty-one successful feeding attempts were observed and large young completed 38 (74.5%) of these attempts.

Production was estimated at 2100 young from 3911 nests in 1973 (.54 young per nest) and 1200 young from 3082 nests in 1974 (.39 young per nest).
ACKNOWLEDGMENTS

The Max McGraw Wildlife Foundation provided financial support for this project. The North Dakota Game and Fish Department supplied fish tag data. Jim Matthews, refuge manager of the Arrowwood National Wildlife Refuge provided assistance in obtaining bands, permits, and access to Chase Lake National Wildlife Refuge. His cooperation was greatly appreciated.

LITERATURE CITED


DEPT OF FORESTRY, MICHIGAN TECHNOLOGICAL UNIV., HOUGHTON, 49931. ACCEPTED 12 SEPT. 77.
EGG VOLUME AS A PREDICTOR OF HATCHLING WEIGHT IN THE BROWN-HEADED COWBIRD

Val Nolan Jr. and Charles F. Thompson

Variations in dimensions or weights of eggs of certain bird species have been correlated with age of female, date, clutch size (e.g. Nice 1937:112-120, Romanoff and Romanoff 1949:61-87; see also Coulson 1963), and more recently with annual environmental conditions (Jenkins et al. 1967:111) and sequence of laying in the clutch (Kendeigh et al. 1956, Murton et al. 1974, Howe 1976, Nolan 1978). Among conceivable explanations for such trends, the most probable appear to be differences in absolute and relative quantities of energy-yielding and other constituents packaged in the egg (see Berg and Bearse 1957). These differences, in turn, should affect size and viability of the embryo and/or hatchling; and at least some of them, therefore, are presumably the products of selection (Howe 1976).

We considered it important to learn how, if at all, egg size is related to hatching size in a passerine and investigated that question in the Brown-headed Cowbird (Molothrus ater). We selected the cowbird for this purpose because data on the size of eggs of brood parasites (Wickler 1963:193-194, Friedmann 1963:21-22) and the size of their young at hatching (Southern 1964) are of interest in themselves. The results demonstrate that a cowbird egg’s length and breadth can be used to predict the weight and probably the overall body size of the nestling produced. Since recent evidence (see below) suggests that correlations comparable to the one presented herein can be expected rather widely among birds, our methods may have general utility in field studies.

METHODS

On the advice of Frank W. Preston (pers. comm.) that volume is “the best single specification of size” of eggs, we selected volume as the parameter to be measured. Considerations of convenience reinforced this decision: volume can be calculated from an egg’s length and breadth, which are easily found. Weight, on the other hand, is hard to obtain in the field and is subject to the added disadvantage that it changes throughout incubation.

The frequently used formula for volume, length × breadth2 × 0.524 (e.g. Romanoff and Romanoff 1949:108), assumes that the egg is an ellipsoid of revolution, an assumption not always justified (Preston 1974). We therefore found true volumes of cowbird eggs that we collected (1970-1976) on and near a study area (described in Thompson and Nolan 1973) outside Bloomington, Indiana, and on the basis of these values calculated a coefficient to replace the 0.524 in the conventional formula. An egg’s actual volume was obtained from 3 weights, those (1) of the egg, (2) of a sealed container filled with distilled water, and (3) of the same container filled with distilled water and the egg.
Weight 1 was subtracted from weight 3 and the difference subtracted from weight 2, yielding the weight and volume of water the egg had displaced (for other details, see Nolan 1978). The mean volume of 45 eggs was 2.890 ml ± (≈ standard deviation) 0.319 ml; extremes were 3.78 ml and 2.34 ml (compare Wetherbee and Wetherbee 1961). The mean value of the coefficients derived from the 45 volumes was 0.515 ± 0.014; extremes were 0.548 and 0.491.

To investigate the relation between egg volume and hatchling weight we used 41 cowbird eggs collected from the same location and over the same period as the sample just described. These we incubated (at 37°C, 60% relative humidity) until they hatched. Volumes (ml) were calculated as equal to length × breadth² × 0.515. The sample was not randomly selected: eggs in nests of certain hosts that we were studying ordinarily were left uncollected, and we made special efforts to include a few unusually large and unusually small cowbird eggs. However, distributions of volumes and hatching weights did not deviate from normal (P ≈ 0.2, Kolmogorov-Smirnov test). Considering the time interval and the area over which eggs were collected, it is unlikely that any female contributed more than one egg to the sample.

Young were weighed within 10 h (usually within a few minutes) of hatching. (Hatching was at all times of day and night; compare the contrary finding by Wetherbee and Wetherbee 1961:156.) Weights were rounded to 1 cg; for several reasons greater precision was unattainable. Post-hatching weight loss varies with time spent in the incubator, and neonates may defecate even though they have not eaten (Wetherbee and Wetherbee 1961). Further, frequency and times of egg turnings varied and incubator temperature and humidity fluctuated slightly (see Rol’nik 1970:307-308, 314-315, 327, 333), all of which could have affected hatching weight.

The foregoing procedures can be simplified by investigators who are not interested in egg volumes and who want only to predict hatching weight from easily measured egg parameters. Obviously, any significant statistical relationship between egg volume and hatching weight will also exist between hatching weight and the product of egg length × breadth², and no constant need be considered.

RESULTS

The weights of young plotted against the volumes of the eggs that produced them (Fig. 1), reveal a close positive linear relationship. The regression equation is Y = -0.05 + 0.78X. Because egg volumes were calculated from a formula and hatching weights were subject to the slight experimental error mentioned, we make no probability statement about the regression. The results of a correlation analysis are r = 0.96, df = 39, P = <0.01.

Mean calculated egg volume was 3.009 ml ± 0.333 ml and mean hatching weight 2.289 g ± 0.271 g (compare Wetherbee and Wetherbee 1961). Extremes of volume were 3.905 ml and 2.411 ml. The largest egg measured 24.2 × 17.7 mm and produced a young bird weighing 3.11 g; the smallest egg, 20.0 × 15.3 mm, produced a young weighing 1.75 g. The mean length of the 41 eggs was 21.49 mm ± 1.10 mm, the mean width 16.46 mm ± 0.61 mm. Although both length alone and breadth alone correlated significantly with hatching weight, neither correlation was as close as that of volume (length, r = 0.75; breadth, r = 0.89).
Fig. 1. Regression of weight of newly hatched Brown-headed Cowbirds on calculated volume (see text) of eggs that produced them. The regression equation is $Y = -0.05 + 0.78X$.

Wetherbee (1961:419–421), in a review of neonatal condition of many North American bird species, calculated neonatal weights as percentages of egg volumes and found that in most species the value is about 75%. The cowbirds in his sample, at 81%, represented an extreme; and Wetherbee considered their deviation a possible adaptation for brood parasitism. The means of our data (first sentence of the preceding paragraph) yield a figure of 76%, which is below many of Wetherbee’s percentages for non-parasitic passerines.

**DISCUSSION**

Discovery of a linear correlation between volume of egg and weight of hatchling in the cowbird might be of narrow interest if that relationship were a specialization associated with parasitic reproduction, but this possibility is
remot. In chickens (Gallus gallus; Halbersleben and Mussehl 1922, Skoglund et al. 1952, Godfrey et al. 1953) and possibly in Red Grouse (Lagopus lagopus scoticus; Jenkins et al. 1967:111) larger eggs produce larger chicks. More recently, positive egg size-hatchling size relationships have been reported in 4 other bird species, 2 of them passerines and 1 an icterid: the Herring Gull (Larus argentatus; Parsons 1970), the Wood Pigeon (Columba palumbus; Murton et al. 1974), the Great Tit (Parus major; Schifferli 1973), and the Common Grackle (Quiscalus quiscula; Howe 1976). Most interestingly, Schifferli (1973) found that weights of Great Tit eggs could be estimated from the formula \(0.527 \times \text{length} \times \text{breadth}^2\) and that the regression coefficient of hatchling weight on egg weight is 0.725. Assuming that cowbird and tit eggs are about the same shape, the striking similarities of Schifferli's formula for weight and his regression coefficient to our formula for volume and our regression coefficient strongly suggest that our data do not reflect a specialization for brood parasitism.

Most investigators named above considered whether egg size and/or hatchling weight affected viability and/or rate of development. In general, advantages for heavier eggs and young were indicated (but see Davis 1975 on the Herring Gull and Skoglund et al. 1952, Godfrey et al. 1953 on chickens).

Reasons for the greater weight of young Great Tits produced from large eggs were thought by Schifferli (1973) to be either larger overall body size or the possession of greater reserves of yolk (see Parsons 1970, Howe 1976), or both these factors. Our inspection of newly hatched cowbirds revealed that bodies, wings, and heads of the heaviest individuals were considerably larger than those of the lightest. Heavy young looked bigger in all respects.

All studies referred to in this section, except those of the Herring Gull, focused on weights of eggs and related these to weights of young. (Schifferli calculated at least some egg weights from their measurements.) We reiterate our view that most workers will find it impractical to obtain egg weights directly, and we conclude by emphasizing the utility of our methods. Especially when data on hatchling size are required on a large scale, the convenient procedure would appear to be to work out a regression equation and then simply to measure eggs.

**SUMMARY**

Known volumes and measurements of eggs of the Brown-headed Cowbird (Molothrus ater) collected near Bloomington, Indiana, revealed that the formula length \(\times \text{breadth}^2 \times 0.515\) produces a good estimate of the volume of these eggs. Volumes of a second sample of cowbird eggs were calculated from measurements, the eggs incubated, and young were weighed shortly after hatching. Calculated egg volumes and hatchling weights were positively and linearly correlated \((n = 41; r = 0.96)\); the regression coefficient of
hatching weight on egg volume was 0.78. The significance of the results and the methods is discussed.

ACKNOWLEDGMENTS

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LITERATURE CITED


Indiana Univ. Dept. of Zoology, Bloomington 47401, and State Univ. College of Arts and Sciences, Geneseo, NY 14454. Accepted 16 July 1977.
BEHAVIOR AND SEX ROLES OF NESTING ANHINGAS AT SAN BLAS, MEXICO

JOANNA BURGER, LYNNE M. MILLER, AND D. CALDWELL HAHN

Presumably, the time and energy each parent devotes to courtship, nest-building, nest-defense, and care of the young is a compromise between its own survival and that of its offspring. The role each sex plays, therefore, contributes greatly to the social system a given species displays. The frequent absence of quantification concerning sex roles can be attributed to the difficulties of identifying individuals (and sexes) and to the time required to collect these data.

We studied the breeding biology of Anhingas (*Anhinga anhinga*) in a mangrove swamp on the west coast of Mexico to determine: (1) their general breeding biology, (2) whether sex role differences occurred, (3) how their behavior compared to that of Anhingas nesting in freshwater, and (4) their relationships with other species nesting in the colony. Males and females were easily distinguished as the species is sexually dimorphic.

Most data on breeding Anhingas have been collected in freshwater swamps in the United States. Anhingas primarily nest in trees in freshwater swamps of shallow, quiet water, although they will nest in mangrove-bordered salt and brackish bays in coastal areas (Palmer 1962, Owre 1967). Meanley (1954) and Allen (1961) have written general breeding biology accounts. Owre (1967) described their adaptations for locomotion and feeding, and Van Tets (1965) compared their display patterns with those of other Pelecaniformes.

STUDY AREA AND METHODS

We made observations on the Pacific Coast of Mexico at San Blas, Nayarit, Mexico (latitude 21°33′N, longitude 105°17′W). The area, in the tropical dry forest zone (Holdridge 1952), contains rivers and estuaries lined with mangrove swamps. The climate of the area is divided into a hot rainy season from April through November and a warm dry season from November through March. The intensive rainy season begins in late June to mid-July and ends in late September to early October (Dickerman and Gavino T. 1969, Dickerman and Juarez L. 1971).

The study area, 2 km northeast of the fishing village of San Blas, has been described by Dickerman and Gavino T. (1969), Dickerman and Juarez L. (1971), and Alden (1969). The principal tree species in the mangrove swamps are *Rhizophora mangle*, *Avicennia nitida*, and *Laguncularia racemosa*. *Rhizophora* grew singly surrounded by open water, whereas *Avicennia* and *Laguncularia* formed groves separated by open channels 5 to 20 m wide. The height of the mangroves ranged from 4 to 7 m with *Avicennia* being the tallest.
Water levels ranged from 50 to 120 cm in the lagoons and channels of the study area. Heavy rains increased water level by as much as 35 cm. Water levels vary from year to year; Mock (1975) worked in this colony in 1974 and reported a seasonal maximum water depth of 90 cm in early July. Nesting starts at the beginning of the rainy season when water levels rise in the lagoons (Dickerman and Gavino T. 1969, Dickerman and Juarez L. 1971).

Our study colony contained approximately 90 pairs of Boat-billed Herons (*Cochlearius cochlearius*), 75 pairs of Green Herons (*Butorides virescens*), 40 pairs of Great Egrets (*Egretta alba*), 50 pairs of Louisiana Herons (*Hydranassa tricolor*), 40 pairs of Anhingas, 25 pairs of Olivaceous Cormorants (*Phalacrocorax olivaceus*), and 20 pairs of Little Blue Herons (*Florida caerulea*). In 1963 and 1964, when Dickerman worked in the area, there were also nesting Snowy Egrets (*Egretta thula*), Black-crowned Night Herons (*Nycticorax nycticorax*), and Yellow-crowned Night Herons (*Nyctanassa violacea*).

We made observations daily during the period from 8 July to 19 August 1975. All species were relatively tame and resettled quickly on nests 5 to 10 m from us, thus, we created little disturbance. We tagged all nests and recorded the following data: clutch size, tree species, height of nest above water, width and depth of nest, leaves in the nest, species of nearest neighbor, and distance to nearest possible open perch site. We checked nests daily during the egg-laying and hatching period and recorded nest measurements and the percentage of leaves in nests at the end of the incubation period prior to hatching.

We selected 3 areas in the colony, having the closest nests, for intensive behavioral observations. One area contained the following nests: 5 Anhingas, 5 Great Egrets, 7 Green Herons, and 2 cormorants; another contained 6 Anhingas, 3 Great Egrets, 2 Green Herons, and 1 cormorant; and the third contained 3 Anhingas, 8 Great Egrets, 4 Green Herons, and 3 cormorants.

We observed in periods of 5 to 8 h, from 05:30 to 13:00 or from 12:00 to 19:00. Three observers recorded data from each of 14 nests for 320 h during incubation and 105 h during the chick phase. We routinely recorded weather conditions, the individual incubating, the presence of its mate, the distance between mates, nest material trips, the distance travelled for nest material, the initiator and recipient of aggression, the winner and loser of aggressive encounters, and behavior during nest relief. During the brooding phase we recorded time, duration, and behavior of feeding sequences. All means are given with one standard deviation. NS indicates that differences between means are not significant.

**RESULTS**

*Breeding chronology.*—The egg laying periods for each species in 1975 are given in Fig. 1. Green Herons were the first to initiate egg-laying (on 30 June), followed by Louisiana Herons, Great Egrets, Anhingas, cormorants, Boat-billed Herons, and Little Blue Herons. The duration of the egg-laying period of each species varied from 12 days in the cormorant, to 22 days in the Great Egret. The duration of egg-laying did not correlate with the number of nests per species.

Anhingas laid eggs from 8–23 July. Precise data on egg-laying in 16
nests indicated a peak in egg-laying from 14 to 16 July, just following a prolonged rainy period from 10 to 13 July. Fifty percent of the eggs were laid from 14 to 19 July. The clutch size (3.89 ± 0.58, range = 2 to 5, n = 16) was similar to the 3.8 reported by Palmer (1962).

*Nest site selection.*—Anhingas nested randomly with respect to the tree species in which their nests were located ($\chi^2 = 0.32$, d.f. = 2, NS); 41% of the pairs nested solitarily in a tree, 34% nested in trees with other species, and 25% nested in trees with only other Anhingas. Generally Anhingas nested in open areas at the top of trees. Cormorants often nested near and in sites similar to Anhingas. Mean nest height above water of Anhingas was 244.8 ± 61 cm, compared to 234.1 ± 51 cm for cormorants, 321.8 ± 61 cm for Great Egrets, and 32.0 ± 21 cm for Green Herons.

Anhingas built 80% of their nests (n = 32) at the junction of the trunk and branches and nested on less substantial branches than those selected by Great Egrets. All 40 Anhinga nests had an exposed perch site nearby ($\bar{x} = 116 ± 52$ cm) that was used and defended by non-incubating mates. Cormorants also selected nest sites near exposed perches.
Three to 6 pairs of Anhingas nested near one another, separated from other such groups by open water and mangrove stands. Anhingas nested closer to conspecifics than predicted by their occurrence (χ² = 11.2, d.f. = 6, p < .001, Fig. 2). Although Anhingas made up only 10% of the colony, they were nearest neighbors to each other 80% of the time. The mean distance to nearest neighbor was 208 ± 178 cm. The distance to the nearest neighbor Anhinga (̅x = 235 ± 178 cm, n = 32) was greater than when other species were nearest neighbors (̅x = 148 ± 100 cm, n = 3), but not significantly so. Nearest neighbors are also the result of differences in habitat preferences. For example, Boat-billed Herons always nested in the prop roots of red mangrove, and thus, never nested near Anhingas (see Burger 1978).

Incubation behavior.—We observed each of 14 Anhinga nests for 320 h during incubation. Anhingas incubate eggs continuously until they hatch. When summed over the entire incubation period, the sexes incubated equal amounts of time (t = 0.62, d.f. = 49, Fig. 3) which agrees with the unquantified statements in the literature (Kendeigh 1952, Meanley 1954, Allen 1961). Mean female incubation time over the entire incubation period was 45%, but female incubation at individual nests ranged from 37 to 65%. Males incubated 55% of the time, and individual males ranged from 35 to 63% (Table 1).

These data can be organized for an examination of daily variations (Fig. 4). From 06:00 to 15:00 there was an equal probability (χ² = 0.32, d.f. =
Fig. 3. Sex role differences in nesting Anhingas. Solid bar indicates female activity, the hatched bar male activity. INC = incubation, A = aggression, NM = nest material trips, BX = amount of time present before nest relief, AX = amount of time present after nest relief, NX = mate present but not incubating, B = brooding and F = number of times chicks are fed.

Table 1
Activity Differences Among Anhinga Nests as Expressed by the Range of Means from 14 Nests

<table>
<thead>
<tr>
<th>Activity</th>
<th>Female</th>
<th>Male</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Grand Mean</td>
<td>Range of Means for Nests</td>
</tr>
<tr>
<td>Incubation (% of time)</td>
<td>45</td>
<td>37–65</td>
</tr>
<tr>
<td>Aggression (interactions per bird for entire incubation period, n = 132)</td>
<td>.5</td>
<td>0–3</td>
</tr>
<tr>
<td>Nest material trips (trips per bird: for entire incubation period, n = 38 trips)</td>
<td>1.0</td>
<td>0–7</td>
</tr>
<tr>
<td>Feeding of young (% of time)</td>
<td>43</td>
<td>38–62</td>
</tr>
</tbody>
</table>
1, NS) of finding a female or male incubating at any nest, but significantly more males ($\chi^2 = 15.3$, d.f. = 1, $p < 0.01$) incubated at sunrise and sunset. For several nights we remained until after dark and returned well before dawn. At all nests the same bird was present after dark and before dawn, and 65% of the time it was the male. The same sex, however, was not always on the nest on successive nights.

When these incubation data are arranged by day of incubation, they demonstrate that males incubate more than females (Fig. 5). We grouped the data by 5 day intervals. Males were incubating for significantly more of the time from days 1–5 ($\chi^2 = 7.30$, d.f. = 1, $p < 0.05$) and 26–30 ($\chi^2 = 14.8$, d.f. = 2, $p < 0.005$). Eggs hatched during the period from day 26 to day 30.

The mean length of completed incubation bouts for females was $2.43 \pm 1.56$ h ($n = 25$) and for males it was $2.67 \pm 1.72$ h ($n = 28$). These data select for short incubation bouts, since the same bird sometimes incubated during a whole 8 h observation period. Therefore, we computed the bouts using both incomplete and complete bouts. The duration of the mean bouts
did not differ \( (t = 0.32, \text{ d.f.} = 154, p < 0.05) \) between females \( (\bar{x} = 3.25 \pm 1.58, n = 196) \) and males \( (\bar{x} = 3.53 \pm 1.58, n = 187) \).

We observed copulations and attempted rapes (made by neighbor males) up to 15 days after the initiation of incubation.

*Nest relief and presence of the non-incubating mate.*—Mates often remained at the nest site when not incubating. The total time females and males were present as non-incubating birds did not differ when summed for the entire season \( (t = 1.22, \text{ d.f.} = 10, \text{ NS}) \). The amount of time a mate was present decreased as the incubation period progressed (Fig. 5). After day 25, a mate returned only to exchange.

The presence of a non-incubating bird indicated 1 of 3 situations: the bird had arrived and would shortly exchange with the incubating bird; the birds had just exchanged; or the bird returned and would leave without exchanging. When analyzed this way, females and males behaved differently
Table 2

Presence and Location of Non-incubating Anhingas Before and After Exchanges

|       | Of Nests | Of Exchanges | | | |
|-------|----------|--------------|--------|--------|
| Time Present (Mean values for nests) | | | | |
| Before | 14 | 239 | 15 ± 7 | 8.5 ± 3 | 3.02 | .05 |
| After | 14 | 245 | 10 ± 10 | 15.5 ± 13 | 1.08 | NS |
| During | 14 | 248 | 19 ± 18 | 12.5 ± 13 | 1.22 | NS |
| Distance | | | | | |
| Before | 14 | 63 | 4.84 ± 5.72 | 3.26 ± 3.10 | 1.4 | NS |
| After | 14 | 55 | 2.84 ± 1.92 | 3.60 ± 2.24 | 1.35 | NS |
| During | 14 | 31 | 6.06 ± 3.06 | 3.76 ± 2.81 | 2.13 | .05 |

"Before" refers to the presence of the bird before an exchange, "after" refers to a bird present after an exchange, and "during" means the bird came and left without exchange. Times are given in minutes, distances in meters. Values are in Mean ± S.D.

(Fig. 3, Table 1). Of the total number of times a mate was present nearby before an exchange (n = 239), 70% of the time it was a female; of the total time a mate was present after an exchange (n = 245), it was a female only 22% of the time. Females were present a mean of 15 ± 7 min before exchanging and remained 10 ± 10 min after exchanging (Table 2). Males were present a mean of 8.5 ± 3 min before exchanging and remained 15.5 ± 13 min after exchanging. Females were present significantly more time each exchange than were males (t = 3.02, d.f. = 10, p < 0.05). Thus, it appears that females came earlier before an exchange, left more quickly after an exchange, and were more apt to return to the nest and to leave without an exchange.

We recorded where mates perched on exposed limbs and later measured these distances. Females and males did not differ in the distance they perched from the nests before and after nest relief (Table 2). The differences between females and males with respect to time and distances present before, after, and without exchanges are not all significant, but combine to form a clear pattern. Females returned earlier before exchanging and remained farther from the nest. After exchanging they remained closer to the nest but left earlier than males. Females that returned without exchanging remained longer but were farther away from the nest than were males.

Behavior during nest relief.—An exchange occurs when the non-incubating bird returns to relieve its mate. Exchanges (n = 197) occurred more frequently at some times of the day than at other times (Fig. 4). More exchanges occurred from 07:00 to 09:00 and from 14:00 to 15:00 than at other times of the day. Few exchanges occurred before 06:00, from 11:00 to 13:00, or after 17:00.
Allen (1961) reported that no noteworthy behavior took place during nest relief, and Owre (1962) described briefly the behavior at nest relief. We found that display behavior at nest relief varied, but vocalizations always occurred. When an exchange was about to occur, the relieving birds always gave a vocalization and then began to approach the incubating bird with its neck outstretched and its head pointing downward, waving gently from side to side (Fig. 6). The incubating bird answered with the same undulating chatter call and extended its head upward toward its descending mate. The pair touched necks gently and frequently interwined their necks slightly, both vocalizing continuously. The relieving bird then lowered its head and walked onto the nest and stood to one side. The relieved bird climbed off the nest onto a nearby branch and often preened before flying off. Variations included bringing nest material: the returning bird vocalized with the material in its bill, thrust its head down, and passed the nest material to the incubating bird. The incubating bird usually climbed off the nest before tucking the material into the nest. Often the incubating bird rigidly extended its neck and head toward its returning mate. Exchanges were similar regardless of which sex was the incubating bird.

Nest structure and maintenance.—Anhingas build their own nests or reuse the nests of other species such as Great Egret, Snowy Egret, and Little Blue Heron (Bent 1922, Meanley 1954, Allen 1961). It is unlikely that Anhingas
reused nests at San Blas since we arrived when only a few nests had been built, and these contained fresh, leafy material; no obviously old nests remained in the colony. Nests were compact masses of twigs (38.6 ± 9.5 cm wide and 16.2 ± 3.3 cm deep, n = 24) at the beginning of incubation. Live mangrove twigs with attached leaves made up 18% (± 15%) of nests. We never observed Anhingas diving for aquatic material and adding it to the nests as did Allen (1961). Nest size (29.0 ± 3.8 cm wide, 15.8 ± 2.4 cm deep, n = 30) and % leaves (\(\bar{x} = 12.2 ± 11\%\)) decreased by the end of the incubation period, as nests gradually fell apart.

Males brought nest material to the nest significantly more often than did females (\(\chi^2 = 16, \text{d.f.} = 1, p < 0.001, \text{Fig. 3}\)). Females made 19% of the nest material trips during this study. Meanley (1954), Allen (1961), and Karraher (1953) reported that males gather all the nest material. Males gathered material significantly closer to the nest (\(\bar{x} = 55.8 ± 56\) m) than did females (\(\bar{x} = 122.4 ± 61.7\) m, d.f. = 38, \(t = 2.21, p < 0.05\)). Males brought back nest material with leaves 75% of the time, whereas females brought back nest material with leaves only 20% of the time. Most (88%) of the 38 nest material trips occurred after nest relief, 9% occurred before nest relief, and 3% occurred at other times. The mean number of nest material trips after an exchange for those exchanges involving nest material trips was 2.88 ± 2.63.

Nest material was gathered throughout the incubation and brooding phases (Fig. 7). Half of the nest material trips made by males occurred during the first 10 days of incubation, whereas in this same period females made no nest material trips. An increase in nest-building occurred just after hatching. Only 5% of male nest trips occurred when they had chicks, whereas 53% of the female trips were made at this time. Thus, females added more nest material during the brooding phase than did the males.

Aggressive behavior during nesting.—Allen (1961) reported that there were not enough aggressive interactions among Anhingas to allow determination of territory boundaries: males showed little response to nearby conspecific males and no response to heterospecifics. However, Van Tets (1965) reported that fighting normally occurs between members of the same sex: males fight over nests and females fight over males. We recorded conspecific aggressive interactions in one area during the study and found that Anhingas defend their nest sites and preferred perching sites. We only recorded conspecific aggression with respect to nesting territories. Aggressive encounters (n = 132), usually brief, involved displacing the intruder. Males were involved in more aggressive encounters than were females (\(\chi^2 = 112.24, \text{d.f.} = 1, p < 0.01\)). During the entire incubation period, each female averaged 0.5 encounters, and each male averaged 7.8 encounters. Our data indicate that males are
the initiators and recipients of most conspecific aggression, that most aggression (75%) is performed by non-incubating birds, and that females are aggressive only toward males. Conspecific aggression decreased as incubation progressed (Fig. 7), and no conspecific aggression occurred after hatching. Non-incubating birds performed 50% of the aggression from day 1 to 10 and 100% of the aggression thereafter.

We recorded interspecific aggression in one study area during the first 20 days of incubation (Table 3). Heterospecific encounters accounted for 25% of the aggression in the nesting group (n = 94). These encounters usually involved the Anhingas displacing the intruder, although twice an Anhinga attacked a cormorant.

We recorded aggressive encounters in an area adjacent to the nesting colony used for roosting by 300 to 400 birds nightly. Eleven % of the roosting birds were Anhingas, yet they were involved in only 2% of the 412 heterospecific encounters and 3% of the 3708 conspecific encounters. Ninety % of the encounters involving Anhingas were conspecific. The mean number of con-
specific aggressive encounters per hour per bird was 0.11 for Anhingas and 0.35 for all other species present. When we added conspecific and heterospecific aggression, Anhingas averaged 0.12 encounters per bird per hour, and all other species averaged 0.44 encounters per bird per hour. Total Anhinga aggression in the nesting colony was similar (0.10 encounters per pair per hour) to that in the roosting areas (0.12 encounters per bird per hour).

**Hatching and chick success.**—During the incubation period 3 nests (with 7 eggs) were dismantled by other Anhingas after being deserted by the nesting pair. Eight additional eggs, lost from nests during the incubation period, no doubt were knocked out of the nests by incubating or exchanging adults. We found them floating below nests. Thus, out of 77 eggs laid in 21 nests there was a 19% egg loss. At least one chick hatched successfully in each of 18 nests.

In 9 nests we had complete data on hatching times of all eggs. Thirty-five of the 36 eggs in these nests hatched. The mean incubation period for the first egg in 14 nests was 27.8 ± 0.91 days (range = 26–29). We followed individual chicks up to 16 days of age before we left the colony. At that time 42 of the 44 chicks hatched were alive. The 2 chicks which died when 8 and 9 days old were the 4th chicks to hatch in 4-egg clutches. At the time we left the colony there were 5 broods of 4 chicks, 5 broods of 3 chicks, 3 broods of 2 chicks, and 1 brood of 1 chick remaining, and all chicks appeared healthy.

**Brooding phase behavior.**—We observed each of 14 nests for 110 h during the brood phase. Males and females spent equal amounts of time in brooding the chicks ($\chi^2 = 0.32$, d.f. = 1, NS, Figs. 3 and 5). One adult brooded the chicks until they were 12 days old while the mate was not present. At 12 days post-hatching, the length of time of each brooding bout began to decrease until by 16 days post-hatching, the mean bout time was 50 min com-

<table>
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<th>Cormorant</th>
<th>Green Heron</th>
<th>Louisiana Heron</th>
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</thead>
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<tr>
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<td>9</td>
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<tr>
<td>Green Heron (7)</td>
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<td>0</td>
<td>0</td>
<td>5</td>
<td>0</td>
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<td>Louisiana Heron (0)</td>
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</tbody>
</table>

* Number of interactions are given as a function of winner and loser.
** Number following the species equals the number nesting in the study area.

Table 3
**Aggression During the First 20 Days of Anhinga Incubation, San Blas, Mexico**
pared to over 3 h when the chicks hatched. Secondly, the parents were no longer present continuously after the 12th day post-hatching. For 3 nests having chicks 12 to 16 days old, the parents were present an average of 91% of the time on day 12, 83% on day 13, 66% on day 14, 58% on day 15, and 41% on day 16. Presumably this reflects the increased time necessary to obtain food for the young. After day 16 post-hatching, a parent returned, fed the chicks, and left before the mate returned.

Both sexes fed the young. Males fed the chicks 57% of the time and females 43% of the time. Forty % of the feedings occurred in the 5 min following nest relief. Chicks fed by thrusting their head into the parent’s throat.

**DISCUSSION**

*The timing of breeding.*—Dickerman and Gavino T. (1969) and Dickerman and Juarez L. (1971) suggested that the initiation of breeding of the birds at San Blas was directly related to the flooding of the mangrove flats. They reported that these lowlands were completely dry prior to the rains in June or early July, and nesting began 3 days after flooding. Under those conditions, flooding was a necessary requisite to nesting as the incubating birds fed in the mangrove swamps and often swam underwater to their nest- ing tree, presumably as an anti-predator device. However, water conditions in 1975 differed. The colony area lagoon contained water throughout the dry season, although the depth decreased, exposing some mudflats a few hundred meters from the colony site (R. Montgomerie, pers. comm.). Food availability in the lagoons may increase with the initiation of the rainy sea- son, and breeding may be associated with these increases. According to local shrimp fishermen, shrimp and small fish do not come into the lagoons until the rainy season. Contrarily, in Campeche, Mexico, nesting in heronries is at the end of the dry season when falling water levels result in concentrating food reserves in small areas (Dickerman, pers. comm.). We believe a de- tailed study of nesting synchrony, nest success, and food reserves in the heronries in these 2 areas would be productive.

A second difference between our data and those of Dickerman and Gavino T. (1969) and Dickerman and Juarez L. (1971) is that in 1975 all species initiated egg-laying in one colony within a 15-day interval. The initiation of nests was, therefore, much more synchronous than in 1964 and 1965 (Dickerman, pers. comm.). It is unclear what environmental factor(s) triggered this occurrence since water levels did not change drastically at this time.

Several heronries in the San Blas area were not synchronous with one another. A heronry with the same species composition located a few km up the San Cristobal River contained young Great Egrets while the Great Egrets
in our study area were still laying eggs. Another heronry farther up the river was intermediate in breeding chronology. Boat-billed Herons in a heronry located on the river to La Tovara laid eggs 2 weeks before Boat-bills laid eggs in our heronry. The synchrony within each heronry was greater than that of the combined colonies. The distances among these colonies are small and certainly within the flying distance of Anhingas, Great Egrets, Snowy Egrets, and the other herons. Perhaps in years when water conditions are favorable, there are sufficient colony sites so that birds nest in heronries at the appropriate behavioral and physiological stage.

Breeding biology and nest success.—The location of the San Blas heronry in a mangrove swamp in association with egrets and herons is typical, although many colonies nest in freshwater swamps (Palmer 1962). Anhingas nest in small groups (this study, Bent 1922, Palmer 1962). Previous studies stated that Anhingas show little aggression (Palmer 1962), little interspecific competition for nest sites (Weber 1975) and no nest defense (Allen 1961). We observed Anhingas defending their nests and their perches from heterospecifics as well as conspecifics. Our long daily observation periods may account for these differences. Anhingas were, however, less aggressive than the herons and egrets that they nested with. The closely related Anhinga melanogaster in Australia also shows little aggressive behavior (Vestjens 1975). We found the incidence of aggression per pair of nesting birds to be similar to that in the nearby roosting assemblage. Both Bent (1922) and Palmer (1962) have noted that Anhingas are aggressive at roosts.

The nests in our study contained live material but no lining. Most reports in the literature indicate that Anhingas line their nests (Sprunt and Chamberlain 1949, Meanley 1954, Allen 1961, Palmer 1962). However, these were all freshwater colonies with more aquatic vegetation. Only Bent (1922) reported a colony with unlined nests. In our study nest material was added throughout the incubation period. Copulation occurred into the second week of incubation and did not cease after the 4th day as reported by Allen (1961).

Few data are available on nesting success in Anhingas. Seven of 10 nests in 1 year and 8 of 20 nests in another year hatched young in a colony in eastern Arkansas (Meanley 1954). This low success rate was attributed to frequent disturbances by humans. In our study young hatched in 13 of the 21 nests followed. We were careful to minimize disturbance in the San Blas colony. Burger has worked in 17 heron, egret, and ibis colonies over the last 3 years, and the birds in the San Blas colony seemed less wary to her than those in any other colony.

Sexual differences in nesting behavior.—In this study males and females shared equally the responsibilities of incubation, brooding, and feeding the
chicks. Males performed 86% and received 98% of the conspecific aggression. Males performed over 80% of the nest material trips. Our results agree in general with the literature, although the role of the female in nest-building and nest defense had been underestimated.

Individual pairs vary in the distribution of responsibilities for incubation, brooding, and feeding. This suggests individual variation in how pairs work out these behaviors. Since no success differences were noted as a result of these variations, we assume that within limits the equality of incubation, brooding, and feeding can be modified. In the 3 nests that failed (after 6, 8, and 9 days of incubation), 1 member of each pair appeared to incubate much more than the other member of the pair (over 75%).

Our data on time and distance of the nonincubating bird from the nest suggest that females show more fear of approaching the incubating male than males show of females. First, females frequently land nearby without exchanging. Second, as males initially build the nest and display there, males are expected to show less “fear” or ambivalence at the nest site. This is further substantiated by the female’s failure to add nest material until after the first 10 days of incubation. Females are less aggressive in general and defend perch sites only sporadically.

### SUMMARY

Breeding behavior and sex roles of nesting Anhingas were studied in San Blas, Nayarit, Mexico during July and August 1975. The Anhingas nested in a mixed species colony of egrets, herons, and cormorants. The egg-laying period for Anhingas was 21 days. Anhingas built nests in the open areas of trees near exposed perch sites and nested closer to conspecifics than to other species.

We observed 14 nests for 483 h during the incubation period. When data were summed for all nests, males incubated for 55% of the time, and females incubated for 45% of the time, although these differences were not significant. However, males did incubate for significantly more time during days 1–5 and 26–30. From 06:00 until 15:00 there was an equal probability of finding a female or male incubating, but significantly more males incubated at sunrise and sunset. Males incubated 65% of the nighttime. At a given nest, the same sex did not always incubate on successive nights.

Males often remained near the nest when not incubating, and there were no sexual differences in time spent nearby. The amount of time a mate was present when non-incubating decreased seasonally. During days 1–5 post egg-laying, mates were present 56% of the time, by days 11–15 they were present 14% of the time, and by day 25 they returned only to exchange. Nest relief, which usually occurred from 06:00 to 08:00 and from 14:00 to 15:00, always involved vocalizations.

Males made significantly more trips for nest material than did females. Males brought nest material with leaves 75% of the time, whereas females brought material with leaves only 20% of the time; 85% of the nest material trips occurred after nest relief. Most (95%) of the nest material trips occurred during the incubation period, although some occurred while chicks were in the nest.
Aggressive encounters were brief and usually involved displacing an intruder. Males performed significantly more aggression (36%) than did females. The non-incubating mate performed 50% of the aggression from days 1–10 and 100% thereafter. Conspecific aggression decreased seasonally. Heterospecific aggression accounted for 25% of the aggressive encounters.

Eighty-one % of the eggs laid in 21 nests hatched. Egg loss occurred through dismantling of the nest and by eggs being knocked in the water from active nests. Of the chicks that hatched, 95% survived until at least 16 days of age. Males and females spent equal amounts of time brooding chicks. One adult brooded the chicks at all times until they were 12 days of age, when the parents began to leave the chicks alone. Both sexes fed the young.

Breeding chronology, success, and sex roles are discussed.

ACKNOWLEDGMENTS

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LITERATURE CITED


POST-FLEDGING BEHAVIOR OF PURPLE MARTINS

CHARLES R. BROWN

The published accounts of the life history and behavior of the Purple Martin (Progne subis) make little or no mention of behavior of adult or young martins immediately after fledging (Bent 1942, Allen and Nice 1952, Johnston and Hardy 1962, Finlay 1971a). Stone (1937:709) noted post-fledging behavior of Purple Martins in New Jersey. Finlay (1971b) reported post-breeding nest defense in adults, but he did not study young martins after they fledged.

Between 1972 and 1977 I located and studied martin broods after they had left their nests in north central Texas. This paper presents a descriptive and quantitative report of post-fledging behavior of young Purple Martins and behavior of associated adults.

METHODS

A substantial amount of this report is based on observations made in 1974 and 1975. Each of the 41 Purple Martin broods at the study colony in 1974–75 were banded with standard aluminum bands painted distinctive colors. Each brood had its own color code. Parents of 20 of these broods had been banded similarly in previous years or during the present study. Parents of 11 additional broods could be identified by distinctive plumage characters. I searched on foot, on a bicycle, and in an automobile for martin broods out of the nest and used 7x and 8x binoculars to observe the birds. I spent much time in daily observation of martins at the study colony in a residential section of Sherman, Grayson County, Texas. Nests in the colony were numbered and watched throughout the season. Twenty martin pairs comprised the colony in 1974 and 21 pairs were present in 1975. Data from only the 1974–75 breeding seasons were used in a quantitative analysis, but observations from 1972 through 1977 were used in forming the descriptive account.

All-purple male martins were termed "adults," and males in first nuptial plumage were termed "subadults." I did not separate adult and subadult females. Young ready to fledge or ones recently fledged were termed "juveniles." The term "fledge" is used here to indicate a young bird's first flight from the nest.

RESULTS

Leaving the nest.—Young Purple Martins that were reared in martin houses which were equipped with ledges or porches beneath the nest hole invariably came out onto the porch 1 to 4 days before fledging. Here they sat, flapped their wings, and were fed. Allen and Nice (1952) state that the parents pull the young off the ledges when time to fledge. I never saw any parent martin attempt to pull off its own young, although if a juvenile from another
nest of different age joined the brood, the parent attacked the newcomer. Shortly before leaving the nest and throughout the post-fledging period, parent Purple Martins could not apparently recognize their own young from others of the same age. Vagrant martins that were not nesting at the time and were simply visiting the colony often tried to pull juveniles off the ledges when the parents were away. Occasionally they succeeded, but more often the juveniles escaped them and retreated inside the nest compartment. These visitors were chased away by the parents when the parents returned. Vagrant subadult males in particular engaged in harassment of juveniles to a great degree.

Normally young Purple Martins first left their nests in the early morning, usually during the first 2 h of daylight. If a juvenile of a brood had not fledged by noon on a given day, it was likely to leave on that day only if disturbed by me or a visiting martin. I recorded only 1 instance of a seemingly-undisturbed juvenile fledging in the afternoon. In 20 instances which I observed, a juvenile first flew from the nest immediately after one of its parents had flown from the nest. The juvenile followed closely behind its parent. At that point many of the resident and non-resident martins at the colony commonly pursued the juvenile. They appeared to attack the juvenile, hitting it on the back with their wings and pecking it on the tail and rump. I observed at least 75 instances of adults attacking juveniles in this fashion. Parents led the juveniles away from the immediate vicinity of the colony and then attacked the pursuing martins and dispersed them.

After the parents led the juveniles away from the colony, the juveniles soon found a perch. Then the parents returned to the nest. On mornings when the young were leaving, the parents seemed very excited and did not feed the young. When at the martin house they were very alert and extremely aggressive toward any other martins that were nearby. Usually 1 young at a time left, although on 6 occasions I saw 2 or 3 juveniles leave the house simultaneously. I occasionally saw broods containing as many as 5 juveniles all leave on the same morning, but in most broods of 3–6 young, all did not leave on the same day. Broods of 6 young often took 3 days to fledge (Table 1).

Assembling the brood.—This was a remarkable phase of post-fledging behavior of Purple Martins, and still it is not clear how brood assembly is accomplished. After leaving the nest, most young martins landed in trees or on utility wires and home television (TV) aerials. A brood when leaving became scattered throughout the neighborhood. At that time the juveniles constantly uttered a “choo-choo” note. Apparently the call helped parents in locating the young, as the juveniles began calling loudly whenever a mature bird flew past.

By mid-afternoon on the day the young left, the parents had assembled
Table 1

<table>
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Mean Number of Martin Young Fledged Per Brood Per Day of Fledging, 1974–1975

their brood on a convenient perch, usually on wires or TV aerials. Here the young remained for the rest of the day and often several days afterward. The parents showed great success in finding and assembling all the members of their brood. Of the 26 broods on which I was able to make post-fledging observations in 1974 and 1975, 20 (76.9%) assembled 100% of their brood.

Observations of marked birds showed that parents were able to gather their own brood even when several nests were leaving on the same morning at a large martin colony. However, the broods mixed somewhat, and “adoptions” by the parents were frequent. I did not collect quantitative figures on adoptions. Parents accepted any young which were within 2 or 3 days of the age of their brood. Since broods returned to the colony to roost in the evenings, the parents reassembled their broods each morning for the first few days after fledging.

The grouping area.—The locations where parent Purple Martins assembled their broods immediately after fledging I termed “grouping areas.” In 1974–75 I located the grouping areas of 26 of the 41 martin broods (63%). The distances of these grouping areas from the study colony are shown in Fig. 1. The remaining 15 broods and their parents were not found after fledging, although I searched within a 1.6 km radius of the colony.

These grouping areas were usually within 1 km of the colony and consisted of 2 or 3 home TV aerials or wires. Thirteen of the 26 broods grouped in clusters of wires around light poles, while the remaining broods grouped largely on aerials. The broods did not seem to be bothered by heavy automobile and pedestrian traffic below them. Eighteen of the 26 broods (69.2%) congregated on wires or aerials near a large open field. The field provided insects for food and an open area for flight. Only once did the parents group their brood within sight of an active martin colony. The habit of broods assembling on wires was noted by Stone (1937:709).

While in the grouping area, broods perched quietly and remained tightly grouped. The juveniles made short flights around the area, but I never saw
Fig. 1. Distances of grouping areas from study colony. Open circle indicates location of colony; closed circles show grouping areas.

one stray from the vicinity. The juveniles spent much time preening and sunning themselves. They continued their "choo-choo" notes while in the grouping area, especially whenever other martins passed by.

Parent martins frequently fed their brood, but they only occasionally sat and preened with the young in the grouping area. However, the parents were probably nearby much of the time, since they arrived to defend their young whenever danger threatened. I do not believe that the parents returned to the martin colony during the day at that time. Male and female parents equally cared for and fed their young out of the nest. In cases when part of the brood left and part remained in the nest, either parent might attend either group almost exclusively, or they might both attend both groups.

Vagrant martins, finding a brood in its grouping area, often harassed it
in the same fashion that vagrants tried to pull juveniles off the ledges of the martin houses. The vagrants that engaged in this activity I termed “raiders.” A raider often perched on the back of a juvenile and pecked and harassed it until it fell off the perch. Then the raider pursued the juvenile and continued to harass it in flight. Raiders were most often subadult males, but adult males and females also behaved this way. When a raider began to harass a juvenile, that young bird stopped calling and sometimes gaped slightly at or feebly pecked at the raider, but the juveniles did little to fend off the raiders and depended on their parents for defense.

Parent martins continued to be highly aggressive and defensive when their brood was in the grouping area. They drove away any raider, and they would not allow any other martins to sit near their young. I also observed parent martins attack Turkey Vultures (*Cathartes aura*), Red-tailed Hawks (*Buteo jamaicensis*), Swainson’s Hawks (*B. swainsoni*), Scissor-tailed Flycatchers (*Muscicora forficata*), Eastern Kingbirds (*Tyrannus tyrannus*), Western Kingbirds (*T. verticalis*), Blue Jays (*Cyanocitta cristata*), Mockingbirds (*Mimus polyglottos*), Starlings (*Sturnus vulgaris*), House Sparrows (*Passer domesticus*), Great-tailed Grackles (*Quiscalus mexicanus*), Common Grackles (*Q. quiscula*), and Lark Sparrows (*Chondestes grammacus*) that sat near the young or flew nearby.

Twice I observed sexual behavior in juvenile martins while they were grouped as broods in the grouping areas. On 16 June 1974 I observed copulation by two 29-day-old juveniles. I could not sex the individuals involved, but I assumed it was not reverse mounting. The young birds were quite clumsy, but one mounted the other in typical Purple Martin fashion. On 7 June 1977 I observed a 30-day-old juvenile, presumably a male, in the “Stooped-Submissive” posture of Johnston and Hardy (1962). This posture consists of flight “with the upper back humped, with head lowered, and with tail held low; the rectrices are abnormally constricted so that the tail resembles a tapered spine.” The juvenile maintained this posture for only 10–15 sec. (Contrary to Johnston and Hardy’s belief, my studies suggest that this posture is sexual, not aggressive behavior.)

Leaving the grouping area.—Broods commonly remained at their grouping areas for 2–3 days after the last young fledged. Extremes were less than 1 day and 5 days, with a mean of 2.5 days (*N* = 26). It appeared that broods left the grouping areas before the juveniles were independent. I did not determine where the broods went after leaving the grouping areas. Most broods left during the early morning. However, they continued to remain near, as many broods kept coming back to the nest to roost at night after leaving the grouping areas. The parents did not return to the colony during the day at that time.
Only once did I relocate a brood after it left its grouping area. In 1974 one brood remained at its grouping area for 5 days. On the 6th day I found this brood grouped on wires along a rural road 2.1 km from their grouping area. This new area was largely open with cultivated fields predominant. I saw other broods in that area, and the juveniles were mingling freely. I suspect that other broods also had arrived there after leaving their grouping areas.

Returning to the nest.—Many Purple Martin broods returned to the nest to roost at dusk each day for a short time after fledging. In 1974–75, 35 pairs led their broods back to the nest to roost for 1 day or more. The 6 pairs that did not bring their young back nested late in the season, and by then most martins were using trees for roosting. The mean number of days after the last young fledged on which a brood returned to roost (N = 35) was 4.85. Extremes were 1 and 12 days.

The broods began returning 45–70 min before dark. In a large colony the broods mingled freely when several were returning at once, and few juveniles actually roosted in their own nest. They separated into their respective broods again the next morning. If, when returning to roost, a juvenile tried to enter a martin nest containing small nestlings or eggs, the owners attacked the intruding juvenile, as did House Sparrows whenever juvenile martins tried to enter their nests. Some juveniles were unable to find a room at the colony to roost in until dark.

The parents’ role in return of the young at night was limited. They initiated the return by leading the juveniles to the colony, but once reaching the colony, the parents could do little to help the young find the correct nest. Sometimes a juvenile followed its parent closely and thus reached the nest when the parent alighted at the nest entrance. In at least 30 cases, female parents seemed to have a more dominant role in the returning than did male parents. On several occasions while watching a brood at its grouping area late in the day, I saw the female parent arrive, feed one of the juveniles, then utter a soft, almost inaudible note similar to the “choo-choo” call of the juveniles. Apparently the female’s call had leadership function, because then the entire family suddenly flew straight to the colony, the female leading. I could usually follow them on a bicycle.

On at least 6 occasions I recorded broods returning to the nest at midday when storms approached. The parents and juveniles behaved much as they did when returning to roost. In most instances the storms were of short duration, and the parents and their broods departed when they ceased.

I detected a correlation of fledging date and number of days a brood returned to roost. The 25 broods that fledged before 15 June in 1974–75 returned a mean of 2.6 days longer than the 16 broods that fledged after
15 June. Purple Martins in north-central Texas begin to exhibit traces of pre-migratory behavior after 15 June, notably by roosting in trees of the neighborhood. This likely accounted for the reduced time of returning for later-nesting pairs.

Feeding.—Stone (1937:709) commented on post-fledging feeding of Purple Martins. During the time spent at the grouping area, broods were virtually dependent on their parents for food. Since most broods left their grouping area a few days after fledging and I could not find them, I had limited opportunity to observe the juveniles begin catching insects. Also, I was not able to determine unequivocally how long after fledging the juveniles were dependent on their parents for food.

By noon on the day the young fledged and after the brood was assembled, the parents began to feed the young. On the first 2 days after fledging, the parents alighted beside the young and fed them. They continued to feed them large insects, such as dragonflies (Odonata) as noted by Stone (1937:709). By the 3rd day the parents often hovered above the perched young and dropped the insect into the juvenile’s mouth. On the 4th day out of the nest the juveniles and parents began in-flight transfers of food, also briefly mentioned by Stone (1937:709). I never saw any young make in-flight transfers before the 4th day out of the nest.

The juveniles apparently initiated the in-flight transfers. Seeing a parent approaching with food, a juvenile flew out to meet the parent. The transfer was made when both juvenile and parent hovered briefly. The insect was either seized by the juvenile while the parent held it, or the parent dropped the insect and the juvenile caught it. If the juvenile failed to catch a dropped insect, the parent seized it before it reached the ground. After the transfer the juvenile returned to its perch, and the parent briefly perched with the young or flew away. Occasionally a juvenile flew out to meet an incoming martin that was not its parent, or the parent did not have food. By the time of the in-flight transfers the parents brought smaller insects, and I never saw a dragonfly transferred in flight. In-flight food transfers are common after the 4th day out of the nest and probably continue until the juveniles reach independence.

While watching broods grouped on TV aerials near a large field, twice I saw a male and female parent, respectively, fly near the young and give the soft “choo-choo” note which was used to lead the young back to the nest. In each instance a juvenile left its perch and followed the parent. The parent led the juvenile over the field, and flying only a few meters above the tops of the grass, the parent apparently began pursuing and catching insects. The juvenile also appeared to pursue insects, but I do not know if it captured any.

Whenever perched juveniles saw another martin approaching, they be-
gan to rapidly quiver their half-opened wings. They did this even if the incoming martin was a raider or another juvenile. The parent with food often fed the individual that started quivering first, but this was not a rule. Wing-quivering preceded a juvenile leaving the perch to transfer food in flight.

I saw several juveniles begin to catch insects on the 4th and 5th days out of the nest. In these instances I carefully watched a flying juvenile with binoculars. By the 4th and 5th days they flew readily. They pursued insects large enough for me to see, and they captured a few, although they seemed to have difficulty in locating insects. They apparently had the speed and coordination necessary to capture insects once found.

Other activity.—Parent Purple Martins started returning to the colony during the day 7–10 days after the young fledged. At that time they sat on wires or martin houses for long periods. Apparently the young were then independent. If their nest had not been usurped by House Sparrows or other martins, the parents displayed post-breeding nest defense, or in rare instances they began a 2nd brood (Brown 1978). Finlay’s (1971b) martins that displayed post-breeding nest defense were not the same birds that nested earlier. I observed both vagrants and past breeders display such behavior. In many aspects this stage closely paralleled martin behavior in early spring when pairs were forming. Males defended a room and courted females, and females visited several males. As the season wore on, post-breeding nest defense became less common, and the birds mainly sat on wires and preened and sunned.

Independent juveniles frequently appeared at the colony at that time. They also sat on wires and preened and occasionally visited the martin houses, but they showed no nest defense behavior.

**DISCUSSION**

It was readily apparent in my study that survival rates of juvenile Purple Martins are quite high for at least 4–5 days after fledging and probably longer. Twenty of the 26 broods I studied in 1974–75 showed a 100% survival rate from time of fledging until they left their grouping areas. The remaining 6 broods lost a member, but I do not know if the lost member actually died or if it was adopted by another family. A high survival rate for nestlings and fledged juveniles is necessary in Purple Martins, since they are specialized secondary hole-nesters, usually raise only 1 brood of 4–6 young, and must compete with House Sparrows and Starlings for nesting sites.

Certain behavior during the post-fledging period contributes to a high survival rate. Juveniles’ following their parents when fledging enables parents to better assemble the brood at a later time. If juveniles fledged when their parents were away, they likely could become lost and scattered. The “choo-choo” notes of the juveniles evidently are helpful to the parents when locating
and assembling the brood. If the juveniles were scattered, too much time and energy might be required to care for them and greater post-fledging mortality of young might occur. The parents’ inability to recognize their own young also has survival advantages. (However, in Bank Swallows [Riparia riparia] parents can recognize their own young and will not care for foreign young [Hoogland and Sherman 1976].) When several martin broods fledge at once, any juvenile is adopted and cared for by parent martins. If a juvenile is separated from its own brood, it can likely find and join another brood nearby. The habit of broods grouping on exposed perches probably serves to assist lost juveniles in finding their own or another brood, although this may not be the primary function of perching in the open.

Returning to the nest to roost at night has very obvious survival advantages. High winds and heavy rains at night could cause severe mortality among juvenile Purple Martins, but this threat is minimized by roosting in the nest. To partially counteract this advantage are the opportunities for broods to become scattered when returning to roost. However, the juveniles are able to regroup at their grouping areas on the following mornings. Perhaps the grouping areas are partially imprinted upon them on the day of fledging.

I can find no explanation of why 63% of the martin pairs (N = 41) assembled their broods in grouping areas within 1 km of the study colony while the remaining pairs and their broods disappeared after fledging. There was no correlation between age of parents or brood size and whether a family grouped within 1 km of the colony. Also, I do not know why the broods in grouping areas similarly disappeared after a mean of 2.5 days.

During post-fledging feeding, the manner of feeding is significant. Feeding by dropping an insect into a juvenile’s mouth from above and transferring food in flight may be important in imprinting insect-capturing techniques upon the juveniles.

A curious aspect of post-fledging behavior in Purple Martins is the activity of raiders. The raiders may serve to increase awareness or reflex actions of the young, thus helping to make the juveniles better able to avoid predators. But raiders that harass juveniles in and out of the nest contribute to scattering of the brood with possible resulting mortality of juveniles if parents cannot find the young. A further disadvantage of this behavior is energy expenditures by juveniles that are harassed and by parents that must fend off the raiders. Parents rarely assembled their brood within sight of an active martin colony; this may have been to minimize disturbance by raiders.

The habit of mature martins pursuing and attacking a fledging juvenile closely paralleled raider behavior. This may be advantageous in keeping the young bird aloft during its initial flight. When many martins are harrassing a flying juvenile, it is very difficult for that juvenile to alight. The young
birds are usually able to survive if kept off the ground on their initial flight. A juvenile finds it very difficult to fly from the ground, and parent martins desert grounded young (Forbush 1929, pers. observ.). Harassment also may be important in directing parents’ attention to a member of the brood that they otherwise might fail to notice, thereby assisting parents in grouping their broods. It is quite probable that juveniles become independent 7–10 days after fledging, since at that time parents return to the colony and sit for great periods. Yet this has not been determined by observations of the young actually becoming independent. I concur with Finlay’s (1971b) suggestion that post-breeding nest defense may imprint the location of future nesting sites.

**SUMMARY**

I studied post-fledging behavior of Purple Martins in north central Texas from 1972 through 1977. Detailed studies were made during 1974 and 1975. This report describes various aspects of post-fledging behavior of juvenile, subadult, and adult martins, including accounts of leaving the nest, assembling the brood, feeding, returning to the nest, and post-breeding nest defense. Grouping areas in which broods assembled after fledging are described, as is the habit of leaving these grouping areas. Certain behavior by adults and young during the post-fledging period likely contributes to a very high survival rate of juvenile Purple Martins during the first 4–5 days after fledging.

**LITERATURE CITED**


BOX 1309, AUSTIN COLLEGE, SHERMAN, TEXAS 75090. ACCEPTED 28 JULY 1977.
NESTING ECOLOGY OF THE PLAIN CHACHALACA IN SOUTH TEXAS

WAYNE R. MARION AND RAYMOND J. FLEETWOOD

Plain Chachalacas (*Ortalis vetula mecalii*) of the family Cracidae range throughout eastern Mexico from central Vera Cruz northward to southern Texas (Delacour and Amadon 1973:91). The range in southern Texas is very restricted and includes only portions of 4 counties within the Rio Grande Valley (Marion 1974). Delacour and Amadon (1973) provided a comprehensive review of the literature on the family Cracidae, but their discussion of chachalaca reproduction was based almost entirely on observations of a few nests of 2 species of *Ortalis*. These species, the Chestnut-winged Chachalaca (*O. garrula*) and the Rufous-vented Chachalaca (*O. ruficauda*), were briefly studied by Skutch (1963) and Lapham (1970), respectively. Earlier reports by Bendire (1892:119–121) and Bent (1932:345–352) provided a brief discussion of the nesting activities of Plain Chachalacas. We present here a more comprehensive nesting study for this species.

METHODS

Our research was conducted between 1959 and 1966 (Fleetwood) and during 1971 and 1972 (Marion) at Santa Ana National Wildlife Refuge, adjacent to the Rio Grande, 19 km southeast of McAllen, Hidalgo County, Texas. Nesting information for 1964, 1965, 1966, and 1971 are emphasized in this paper. We obtained reproductive data from wild birds, live-trapped birds, captive birds, and dead birds.

All birds captured during 1971 and 1972 were sexed by methods reported earlier (Marion 1977) and sex ratios are summarized in this report. Chachalaca traps were assumed to be unbiased in attracting either sex. Gonadal development is also reported for birds sacrificed during 1971 and 1972. Reproductive organs were fixed and preserved in AFA solution (Mosby et al. 1969:265) for further examination. Testes and ovaries were trimmed of extraneous tissue and dried on paper towel until all evidence of external moisture was removed. They were then weighed to the nearest 0.1 mg. Ovaries were examined using methods described by Meyer et al. (1947).

Data recorded for each nest observed during field studies included a nest site description involving measurements of the diameter of the nest, species and diameter (DBH) of the supporting tree, distance to water, and height of nest. Nest height was measured with a 6.1 m pole marked off at 0.3 m intervals. This pole, divided into 1.5 m sections for portability, had a mirror at one end which was used to observe nest contents. Nests in taller trees were inspected by climbing.

Clutch sizes were calculated from incubated clutches of eggs and incubation periods were determined where nest history was carefully observed from beginning to end. Egg hatchability was derived from successful nests with complete clutch counts. Eggshells from hatched eggs were easily recognized because they had one end removed by circular
pipping and membranous tissue firmly attached inside. Eggs destroyed before hatching lacked firmly attached membranes and shells were often unevenly fragmented.

Nesting success was determined using nests for which the complete history was known. Nests from which at least 1 egg hatched were considered successful. Nest failure was generally classified as either due to abandonment or to destruction depending on the appearance of the nest and its contents.

Abandoned eggs typically were cool and remained in the nest for some time. Nest destruction was characterized by physical fragmentation of eggs and/or nest (mammals), complete removal of all evidence of eggs and shells (snakes), and unbroken eggs knocked to the ground (wind damage) from the flimsy, shallow nests. The thick-shelled eggs rarely broke when they hit the ground and whole eggs, found beneath a nest, were assumed to have fallen because of wind.

RESULTS AND DISCUSSION

Pairing and sex ratios.—Pair formation begins while Plain Chachalacas are still in winter feeding flocks. Activity levels and loud calling increase considerably in February and March prior to the breeding season. Loud raucous calling is apparently associated with establishment and maintenance of pair bonds, which appear to be monogamous. In 1971, 66 males and 78 females were live-trapped; this was equivalent to a sex ratio of 100 males:118 females. The next year, 35 males and 43 females were captured, or a ratio of 100 males:122 females. Chi-square values of 1.0 and 0.8 (1971 and 1972, respectively) indicated that these sex ratios were not significantly (P > 0.05) different from a 1 male:1 female ratio. No evidence was found to support a strict 1 male:2 females ratio during courtship, as reported by Bent (1932:347).

Gonadal development.—Average testes weights for 48 male Plain Chachalacas collected during all months of the year indicated that the left testis is slightly larger than the right one (125.1 ± 122.4 mg and 102.8 ± 107.3 mg, respectively). The annual cycle in testicular development revealed that the testes weight/body weight ratio was smallest in December and January and largest in March and April (Table 1). Recrudescence and regression of testes was apparently maximum in late February and early May, respectively, but the small sample size restricts further discussion.

In all 102 female specimens examined, only the left ovary was present. Seasonal variation in development of ovaries also was characterized by enlargement during the spring and regression during the summer and fall (Table 2). Peak in ovarian development occurred during April and May when the ovaries had average weights of 3227 ± 4902 and 1099 ± 417 mg, respectively. High variability associated with these mean values was possibly due to the presence of subadult females (which may or may not breed during their first year) in the sample or a lack of breeding synchrony in adults.

Postnuptial regression of ovaries was rapid. Ovaries from 2 (1-year-old) captive females, sacrificed 26 days after laying the last of 19 eggs, weighed
Table 1
Seasonal Variation in Testes Weight of Plain Chachalacas, 1971-72

<table>
<thead>
<tr>
<th>Month</th>
<th>N</th>
<th>Mean Weight* (mg ± SD)</th>
<th>Range</th>
<th>Testes Weight/Body Weight (× 1000)</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>3</td>
<td>24 ± 16</td>
<td>14-42</td>
<td>0.04</td>
</tr>
<tr>
<td>February</td>
<td>2</td>
<td>245 ± 263</td>
<td>59-431</td>
<td>0.44</td>
</tr>
<tr>
<td>March</td>
<td>4</td>
<td>360 ± 102</td>
<td>211-421</td>
<td>648.40</td>
</tr>
<tr>
<td>April</td>
<td>9</td>
<td>435 ± 329</td>
<td>62-545</td>
<td>802.60</td>
</tr>
<tr>
<td>May</td>
<td>2</td>
<td>546 ± 12</td>
<td>537-554</td>
<td>0.89</td>
</tr>
<tr>
<td>June</td>
<td>2</td>
<td>404 ± 13</td>
<td>395-413</td>
<td>0.75</td>
</tr>
<tr>
<td>July</td>
<td>2</td>
<td>314 ± 154</td>
<td>205-423</td>
<td>0.06</td>
</tr>
<tr>
<td>August</td>
<td>7</td>
<td>207 ± 124</td>
<td>69-451</td>
<td>0.37</td>
</tr>
<tr>
<td>September</td>
<td>2</td>
<td>86 ± 38</td>
<td>59-113</td>
<td>0.14</td>
</tr>
<tr>
<td>October</td>
<td>6</td>
<td>69 ± 30</td>
<td>37-109</td>
<td>0.10</td>
</tr>
<tr>
<td>November</td>
<td>6</td>
<td>60 ± 39</td>
<td>24-112</td>
<td>0.09</td>
</tr>
<tr>
<td>December</td>
<td>3</td>
<td>35 ± 18</td>
<td>23-55</td>
<td>0.06</td>
</tr>
</tbody>
</table>

* Represents the mean weight of the pair of testes for each bird.

only 183 and 178 mg. Ruptured follicles were easily observed on ovaries of chachalacas collected within 2 weeks after ovulation. After 5–6 weeks, regression of post-ovulatory follicles was so complete that many could not be distinguished. Ovaries of these 2 captive females had only 9 tiny ruptured follicles (6 on the ovary from 1 bird and 3 on the ovary from the other). Unless ovaries are examined within 2–3 weeks after ovulation, post-ovulatory follicles are apparently poor indicators of egg laying histories of Plain Chachalacas.

Age at sexual maturity.—Although many gallinaceous birds breed during their first year (Van Tyne and Berger 1959:273), it has been reported (Grzimek 1972:449) that many cracids do not breed until their second breeding season. Several chachalacas that appeared to be subadults (Marion 1977) were collected during the breeding season. Some females had enlarged ovaries and ruptured follicles while others had considerably smaller reproductive organs. These observations suggested that some subadult females bred during their first year; others apparently did not. Inaccuracies associated with aging older subadult females (Marion 1977) made it difficult to determine the ratio of breeders to non-breeders. Similarly, accurate determination of the proportion of breeding subadult males was restricted by difficulties encountered in aging males during the breeding season. During this time, the majority of sacrificed males had enlarged testes, but considerable variation existed in testes size (Table 1).

Captive young chachalacas had the potential for reproduction during their
first breeding season. Two captive females mentioned earlier began laying eggs on 26 April 1972, when they were approximately 10 months old. Since 2 eggs were often laid on the same day, both females obviously participated in egg laying. Captive females failed to incubate their eggs. Plain Chachalacas are generally single-brooded but laid additional clutches when eggs were removed or destroyed. Four different clutches totaling 19 eggs were laid by each of the 2 captive females in 1972. Recycling time between clutches was 20–25 days; the last egg was laid on 23 July 1972.

At least 3 incubated eggs from the first 2 clutches contained embryos, indicating that 10-month-old males successfully bred females of the same age. Social mechanisms among wild chachalacas may inhibit young males from breeding during their first year, but data are lacking.

**Breeding season.**—The first chachalaca nests of the season were typically found in April. Sennett (1878:52) and Davie (1889:154) also reported finding the first nests of this species in the Rio Grande Delta during April. Earlier nests do occur, but they are rare. Observation of a chick (about 2 days old) on 24 April 1972 suggested that at least one egg must have been laid and incubated during the last week of March. The incubation period is approximately 25 days. In captivity, Plain Chachalacas have laid eggs as early as the middle of January (P. James, pers. comm.).

The first chachalaca chicks are usually observed in May. Hatching dates were accurately determined during 1971 for 19 nests: the earliest, median,
and latest hatching dates recorded were 10 May, 23 June, and 14 August, respectively. If the initial nest or young are destroyed early in the breeding season, wild chachalacas occasionally renest; this has occurred as late as September or October. On 5 November 1972, juvenile birds less than 1 month old (estimated according to their size) were observed at Santa Ana Refuge and Bentsen-Rio Grande State Park. These observations provided indirect evidence that nesting during the 1972 breeding season occurred in October. Most nesting activity, however, was completed during May, June, and July.

_Nest site description._—Plain Chachalacas are somewhat unique among gallinaceous game birds since they nest exclusively in trees, or vines supported by trees. Of 209 nests examined, 204 (98%) were in trees and 5 (2%) were in vines supported by trees. Mean height above the ground for 192 nests was 3.55 ± 1.45 m (0.9–10.0 m). Heinroth (1931) suggested that the typical tree-nesting habit of cracids was due to frequent flooding of areas inhabited by these birds.

Nineteen tree species were used for nesting, with cedar elm (_Ulmus crassifolia_), huisache (_Acacia farnesiana_), sugarberry (_Celtis laevigata_), anacua (_Ehretia anacua_), and Texas ebony (_Pithecellobium flexicaule_) accounting for over two-thirds (22, 16, 13, 9, and 8%, respectively) of 209 nesting sites. Other trees and vines used, in decreasing frequency, were coma (_Bumelia lanuginosa_), granjeno (_Celtis pallida_), Wright’s acacia (_Acacia wrightii_), Mexican ash (_Fraxinus berlandieriana_), Texas persimmon (_Diospyros texana_), Brasil (_Condalia hookeri_), tepeguaje (_Leucaena pulvulenta_), colima (_Xantholylum jagara_), retama (_Parkinsonia aculeata_), Texas sandbar willow (_Salix interior var. angustissima_), honey mesquite (_Prosopis glandulosa_), guayacan (_Porlieria angustifolia_), guajillo (_Acacia berlandieri_), and Texas virgins bower (_Clematis drummondii_).

These trees were highly variable in size, with an average diameter (DBH) of 18.0 ± 17.2 cm (range 1.3–78.7 cm). The majority (85%) of trees containing nests were living and were draped with Spanish moss (_Tillandsia usneoides_) and tangled vines (_Serjania brachycarpa_ and _Cocculus diversifolius_) that commonly supported and concealed nests. Nests also were located in crotches of trees or forks of horizontal branches. Occasionally, no nest structure at all was used: eggs were laid (and incubated) on tree stubs, on bare crotches of trees, and on horizontal portions of broken limbs.

We found no evidence of Plain Chachalacas nesting in colonies as suggested by Sutton and Pettingill (1942:12). Adjacent nests in close proximity (within 10–30 m) to each other were apparently not used simultaneously during the breeding season and this undoubtedly alleviated conflicts between adjacent breeding males defending nest sites.
**Description of nests.**—Nests were typically small and flimsy because Plain Chachalacas nest extensively in rejuvenated nests or nests of smaller birds, including the Yellow-billed Cuckoo (*Coccyzus americanus*), the Curve-billed Thrasher (*Toxostoma curvirostre*), and the Groove-billed Ani (*Crotophaga sulcirostris*). Most nests appeared to be too small to support a clutch of large eggs: the average maximum diameter (nests were usually oblong) of 42 nests was 21.7 ± 6.4 cm (range 11–34). Frequent wind damage (17% of nest and egg destruction) was undoubtedly due to the instability and small size of nesting structures. Plain Chachalacas were never observed actively building a nest or carrying nesting materials. Nests were composed of a variety of readily available plant materials, including twigs, Spanish moss, vines, and leaves. Nests were occasionally used more than once during the breeding season and from year to year. Three of the 59 active nests (5%) examined in 1971 were reoccupied. Whether these observations represented renesting attempts by the same pair or initial nesting attempts by another pair was unknown.

**Description of eggs.**—Plain Chachalaca eggs are relatively large and have thick, buffy-white and roughly granulated eggshells. These white eggshells, initially unmarked, often become stained by nesting materials in wet weather. Egg shape varies from short ovate to elongate ovate. Size is large in relation to bird size. Mean egg measurements were: length 58.0 ± 2.2 mm (range 51.0–63.7 mm), width 41.0 ± 1.5 mm (range 37.5–49.0 mm), and weight 56.0 ± 6.3 g (range 42.5–70.9 g) obtained from 129, 130, and 89 eggs, respectively.

**Clutch size.**—Average clutch size for 158 complete clutches was 2.88 ± 0.43 eggs (Table 3). Only 3% (5 of 158) of the completed clutches contained 4 eggs; none contained only 1 egg.

Egg laying occurred on alternate days until the clutch was complete. A normal clutch was laid in about 5 days. Nests occasionally contained more than the normal number of eggs, suggesting that more than 1 female used the nest. One nest of 5 eggs was discovered in 1971; 2 of these eggs were laid in an interval of less than 18 h, indicating that more than 1 female contributed to the clutch. This nest was incubated until it was upset by strong winds.

Fleetwood and Bolen (1965) reported a Plain Chachalaca nest that contained 9 eggs. The 9 unincubated eggs in this nest were apparently laid by 4 females. “Dump nests” like these are rare and not severely detrimental to the reproduction of this species.

Nesting observations during 1972 provided positive evidence that 1 nest was used twice by the same pair. This marked pair laid an initial clutch of 3 eggs in late April. These chicks hatched and left the nest on 10 May. Later, the
pair was observed on 3 occasions (12 May, 13 May, and 29 May) without young. A severe thunderstorm the night of 10 May 1972 probably killed the chicks soon after they left the nest. In early June, this pair again nested in the same nesting structure. The second clutch of 2 eggs hatched and both young left the nest before 3 July 1972. No further observations of this marked pair and young were obtained.

Egg production in captive chachalacas commonly exceeds normal production in wild birds. In addition to 2 captive females (approaching a year old) laying 19 eggs, another captive flock (including 4 adult females) laid nearly 100 eggs in 1972 (P. James, pers. comm.). A third captive flock of approximately 60 pairs also laid many more eggs than the normal clutch, depending upon existing moisture conditions. When damp conditions prevailed during the breeding season, many eggs were laid. During drier times, however, egg production was severely curtailed (F. Wied, pers. comm.).

Incubation.—Observations at the nest site indicate that incubation begins within hours after completion of the clutch and only the female incubates. She sits motionless and leaves the nest reluctantly when disturbed. Departure from and return to the nest are typically accomplished quickly and quietly. During the day, incubating females left the nest for brief periods (15–30 min) to feed, but apparently incubated continuously at night. The breeding male was never observed bringing food to his mate; he was observed to remain nearby and to defend the nest site from conspecifics. The incubation period, measured for 6 clutches of eggs in 1971, was 25.3 ± 1.0 days (range 24–27 days). The 25-day average incubation period was slightly longer than those previously reported for this species: 21 days (Grzimek 1972:448), 22 days (Bent 1932:348), 22–24 days (Kendeigh 1952:194), and 24 days (Delacour and Amadon 1973:15).

Hatching.—Hatching of chicks was synchronous. Pipping began approximately 24 h prior to hatching and chicks retained the white egg tooth for 6–10 days after hatching. Egg hatchability was 92% of 249 eggs in successful nests with complete clutch counts (Table 3).

Chicks left the nest within 2 h of hatching. Overall success from 455 incubated eggs was 50% with the average number of chicks per successful nest (N = 89) being 2.5 (Table 3). As the down dried and the last egg was hatching, the precocial chicks actively crawled around in the nest and on top of the mother. The adult male rarely visited the nest during hatching, but watched intently from a nearby perch. After all young hatched, the mother descended to the ground and, with a clucking vocalization, urged the chicks to follow. In descending to the ground, the chicks leaped from the nest and clung to branches and vines as they tumbled downward. After joining the
Table 3

Plain Chachalaca Nesting Summary from Santa Ana National Wildlife Refuge for 1964–66, and 1971

<table>
<thead>
<tr>
<th>Year</th>
<th>1964</th>
<th>1965</th>
<th>1966</th>
<th>1971</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clutch size</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. incubated eggs</td>
<td>133</td>
<td>123</td>
<td>88</td>
<td>111</td>
<td>455</td>
</tr>
<tr>
<td>No. incubated clutches</td>
<td>46</td>
<td>43</td>
<td>31</td>
<td>38</td>
<td>158</td>
</tr>
<tr>
<td>Mean*</td>
<td>2.89 ± 0.43</td>
<td>2.86 ± 0.47</td>
<td>2.84 ± 0.45</td>
<td>2.92 ± 0.36</td>
<td>2.88 ± 0.43</td>
</tr>
<tr>
<td>Range</td>
<td>2–4</td>
<td>2–4</td>
<td>2–4</td>
<td>2–4</td>
<td>2–4</td>
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<tr>
<td>Egg Hatchability</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. successful nests</td>
<td>16</td>
<td>26</td>
<td>24</td>
<td>23</td>
<td>89</td>
</tr>
<tr>
<td>No. eggs</td>
<td>44</td>
<td>72</td>
<td>67</td>
<td>66</td>
<td>249</td>
</tr>
<tr>
<td>Percent hatched</td>
<td>93</td>
<td>97</td>
<td>94</td>
<td>82</td>
<td>92</td>
</tr>
<tr>
<td>Nesting Success</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. nests with complete history</td>
<td>25</td>
<td>37</td>
<td>35</td>
<td>38</td>
<td>135</td>
</tr>
<tr>
<td>Percent successful</td>
<td>60</td>
<td>70</td>
<td>69</td>
<td>61</td>
<td>65</td>
</tr>
<tr>
<td>No. of chicks leaving nests</td>
<td>40</td>
<td>70</td>
<td>61</td>
<td>53</td>
<td>224</td>
</tr>
<tr>
<td>Mean no. to leave successful nests</td>
<td>2.5</td>
<td>2.7</td>
<td>2.5</td>
<td>2.3</td>
<td>2.5</td>
</tr>
</tbody>
</table>

* ± one standard deviation.

mother on the ground, chicks entered the underbrush where they were difficult to observe.

Nesting losses.—Nesting success of Plain Chachalacas was 65% of 135 nests with complete histories over the 4 years, 1964–66 and 1971 (Table 3). Although the nests were usually inconspicuous, over a third of those observed were destroyed or abandoned (30 and 4%, respectively). Agents of destruction were not obvious and determination of causes of nesting losses was somewhat arbitrary. Mammalian predators, such as raccoons (Procyon lotor) and oppossums (Didelphis marsupialis), were apparently responsible for approximately 44% of the nesting losses.

Snakes swallowed entire clutches of eggs, leaving no trace in the nest or on the ground. For this reason, the detrimental impact of snakes on nesting was probably underestimated. Texas indigo snakes (Drymarchon corais ebreennis) have been found that swallowed whole chachalaca eggs (D.
Blankinship, pers. comm.). Snakes were the apparent agents of destruction for approximately 25% of the unsuccessful nests. Eggs were apparently shaken out of approximately 19% of unsuccessful nests by strong winds. In addition, discovery of 5–10 randomly dropped eggs in March and early April each year was not uncommon and an effort was made not to include such eggs in this calculation. Causes of loss were unknown for the remaining 12% of unsuccessful nests.

Care of young.—Observations of family groups indicated that chicks were brooded by both parents. The precocial chicks were observed feeding and roosting with the adult pair at various stages of early development. Within a week of hatching, chicks exhibited great agility in climbing through shrubs and trees. Observations of captive chicks indicated that they were able to jump and fly at least 1.3 m at 6 days of age. Rapid rates of growth and development were previously reported by Marion (1977).

SUMMARY

Nesting ecology of the Plain Chachalaca in the Lower Rio Grande Valley of Texas was investigated during the mid-1960’s and early 1970’s. Pairing and strengthening of pair bonds apparently occur in the late winter; the sex ratio approximates 1 male:1 female, and Plain Chachalacas are apparently monogamous. Gonads enlarge rapidly during early spring; testes size peaks in March and April and ovaries are largest in April and May. Nesting begins in April and is usually completed in July or August. Chachalacas are apparently capable of breeding during their first year, but the incidence of this occurring in wild birds remains unknown.

Plain Chachalacas use flimsy nests supported by a variety of native trees, shrubs, and vines. The mean clutch size for 158 complete clutches was 2.88 ± 0.43 eggs. Incubation by the female takes approximately 25 days, and overall egg hatchability for 249 eggs was 92%. Nesting success for 135 nests over the 4-year interval was 65%; major causes of nest failure included mammalian predators, snakes, and wind damage. Chicks left 47% of the nests in which eggs were incubated and these successful nests (N = 89) produced an average of 2.5 chicks per nest. Chicks are extremely precocial and leave the nest within hours after hatching.

ACKNOWLEDGMENTS

Mr. Cruz Martinez was helpful in locating and observing nests. Others assisting with fieldwork were D. Dolton, S. Johnston, and A. McGrew. P. James and F. Wied provided valuable information on their captive flocks of chachalacas. The U.S. Fish and Wildlife Service and Texas Parks and Wildlife Department granted permission to band, color-mark, and collect birds.

The senior author received financial assistance from the Caesar Kleberg Research Program in Wildlife Ecology at Texas A&M University. Sincere thanks go to W. H. Kiel, Jr. for his advice and encouragement, and to K. A. Arnold, J. D. Dodd, T. M. Ferguson, and J. G. Teer. This is Texas Agricultural Experiment Station Technical Article No. 13169.
LITERATURE CITED


SPATIAL RELATIONSHIPS IN PERCHING BARN AND CLIFF SWALLOWS

ANNE E. HUTTON

Many investigators (e.g. Marler 1956, Crook 1961, Sparks 1964) have conducted quantitative investigations of spatial relationships among captive birds. Although there have been observations of spacing in free-ranging birds (Burckhardt 1944, Condor 1949, Emlen 1952, Hediger 1955, Swinebroad 1964), few quantitative studies have been done in the field. Miller and Stephen (1966) used the nearest-neighbor model of spatial distribution proposed by Clark and Evans (1954) to analyze distances between foraging Sandhill Cranes (Grus canadensis). Grubb (1974) investigated the individual distance (i.e., the closest distance an individual can approach another without resulting avoidance or aggression, Hediger 1950) of Herring Gulls (Larus argentatus) by marking intervals on a plank where they commonly perched.

The spatial regularity of Barn and Cliff swallow (Hirundo rustica and Petrochelidon pyrrhonota) flocks has been reported by Condor (1949), Emlen (1952), and Hediger (1955). I investigated quantitatively the spatial relationships within flocks of these species and studied behavioral mechanisms which maintain or modify spatial relationships.

METHODS AND MATERIALS

Field methods.—Observations of Barn and Cliff swallows were made from 14 July to 19 September 1975 near Saffordville, Chase County, Kansas, where both species flocked together on barbed wire fences. Barn Swallows nested in a culvert there; 15 to 50 birds were present until 12 September. From 22 to 1000 Cliff Swallows (mostly immatures) gathered there, possibly as a pre-migratory flock, from 14 July to 21 August.

Sections of the fence most frequently used by both species were marked at 13 cm intervals with yellow paint. Birds flocked along these fences from sunrise until late morning, and then again in the evening. Observations were made from a parked vehicle from 05:30 to 09:30, and twice from 18:00 to 20:00. Perched flocks flew as cars passed and then reassembled immediately; a parked car did not seem to modify the birds’ behavior.

Photographs, motion pictures, and field notes were used to record interactions and the distribution of birds on the marked fence. Observations and estimates of distances between birds were made from 5 to 15 m away using 7 × 35 binoculars. For 46 field estimates, there was an average difference of 3.0% when compared to corresponding 35 mm slide measurements.

Film analysis.—Slides were projected from a distance of 3 m (the projected image was 70 × 32 cm). The outline of each bird, the location of its feet, and the marked
fence were traced onto paper. Motion pictures were viewed in slow motion, and stopped periodically to make tracings. Distances from the midpoint between one bird’s feet to the midpoint between the adjacent bird’s feet, and the distances between marks on the fence were measured from the tracings. To reduce error due to parallax, the closest visible marks to the birds were used for calibration. Actual distances between birds on the wire (hereafter referred to as “perch intervals”) were calculated using a ratio of the true and measured distances between fence marks.

**Individual distance analysis.**—I assumed that all interactions between swallows were due to spatial violations, although dominance, age, activity, sex, and other factors were probably sometimes involved (Marler 1956, McBride 1964). Three possible results of interactions were recorded: (1) the incumbent flew or retreated, (2) the approaching bird flew or retreated after the incumbent gave a threat display, or (3) the approaching bird discontinued its advances, but remained where it was when the incumbent displayed. Individual distance was considered to be violated in the first 2 cases because the incumbent either retreated or its display effectively removed the aggressor from within its individual distance. In the third case, the approaching bird was assumed to have stopped at the incumbent’s individual distance; no further aggression was demonstrated. In all 3 cases, the closest distance between birds was recorded. Perch intervals were not recorded if the approaching bird retreated when the incumbent gave no display. Encroachment of individual distance in this instance was not evident, although unrecognized signs of communication may have resulted in the approacher’s retreat.

**RESULTS**

**Spatial distribution.**—Frequency distribution curves of perch intervals were significantly skewed to the right for both species (Fig. 1A and B; $g_1$ test, Sokal and Rohlf 1969, $P < 0.001$), and for interspecific spacing between individuals in mixed-species flocks (Fig. 1C; $g_1$ test, $P < 0.01$). There was an abrupt drop in percentages at the shorter perch intervals and a gradual decline at the larger intervals. The 3 distribution curves differed significantly (log transformation and analysis of variance, Sokal and Rohlf 1969, $P < 0.001$). Interspecific spacing was more irregular and perch intervals were at larger distances than in intraspecific spacing; the mean (48.6 ± 25.5 cm) and the mode (35–39 cm) of the former were larger than for either species (Barn Swallow, $\bar{x} = 28.2 \pm 17.5$ SD; Cliff Swallow, $\bar{x} = 34.5 \pm 20.5$ cm).

The mean individual distances of Barn and Cliff swallows were significantly different ($t$-test, $P < 0.005$). Both species exhibited narrow ranges and prominent peaks (Fig. 2). The mode occurred at 12 to 13 cm for the Barn Swallow, and at 10 to 11 cm for the Cliff Swallow (Barn: $\bar{x} = 11.7 \pm 3.9$ cm; Cliff: $\bar{x} = 9.3 \pm 3.1$ cm). Although the individual distance appears to be fairly well defined for these species, it is not absolute since conflicts occurred outside these intervals.

Eight interspecific interaction distances were recorded; Barn Swallows
Fig. 1. Frequency distribution of perch intervals for the Barn and Cliff swallows. Abscissa numerals indicate the beginning of an interval.

were the incumbent in all 8 interactions. The interspecific interactions occurred at the shorter perch intervals ($\bar{x} = 14.1 \pm 3.4$ cm), as did the individual distance interactions. The incumbent Barn Swallows appeared to defend their individual distance against Cliff Swallows as well as conspecifics; there
Fig. 2. Distribution of interactions in maintenance of individual distance. Black: approaching bird remained after the incumbent displayed. Shaded: approaching bird retreated. White: incumbent retreated.

was no significant difference between these interspecific distances and the Barn Swallow’s individual distance (t-test, $P > 0.10$). The former were significantly different from the Cliff Swallow’s individual distance (t-test, $P < 0.001$).

Behavior related to spacing.—Spacing between swallows was established
by direct flight approaches, hovering, and displacement of perched birds; subsequent spatial adjustments were made by sidling, which sometimes involved agonistic interactions. Agonistic displays were similar for both species and were exhibited during establishment and adjustment of spacing. Since birds sometimes landed at locations previously rejected by others, spacing may not be the only factor involved in perch selection. Most new arrivals remained motionless for several seconds before initiating preening, or aggression toward adjacent birds, and they displayed a submissive posture if neighboring birds were close.

Head orientation was important in setting up and maintaining distances between birds. On one occasion, a preening bird intermittently pecked at another whenever the adjacent bird’s head turned toward it. Although a gaping mouth was directed toward opponents during threat displays, it was turned away during “yawning” movements in preening. Submissive birds directed their bills outward.

Maintenance of distances between birds was dependent on the birds’ attentiveness. Conflicts within the individual distance that resulted in the incumbent’s retreat (Fig. 2) occurred when an approaching bird was able to sidle unusually close to an incumbent preoccupied with preening or “sleeping.” These birds often sidled to within a body’s width of the preoccupied bird. When the approaching bird’s presence was noticed, the incumbent flew; if unnoticed, it seemed to advertise its presence by pecking at the incumbent. If the preoccupied bird noticed the approach before the intruder was close, an aggressive response usually caused the approacher’s retreat.

Swallows commonly moved apart prior to, or during preening; this probably lessened conflicts and interference from adjacent birds. Only 2 cases of contact during preening were observed; both resulted in avoidance (1 after a brief conflict).

Adult birds in a submissive posture and young birds sometimes perched within the individual distance without being attacked. Fledgling Barn Swallows sidled over and directed a food begging display (similar to adults’ agonistic gaping) toward any bird perched nearby, or pecked a neighbor’s wing or tail. Adults were very tolerant of young birds and usually retreated or ignored their approaches and displays.

**DISCUSSION**

The similarities of interaction distances and approach and agonistic behaviors make possible the formation of mixed-species flocks, and account for their apparent spatial regularity. The skewed perch interval distributions indicate that within a species, swallows, like Sandhill Cranes (Miller and Stephen 1966), tend to perch at or near the minimum approachable distance.
Barn and Cliff swallows did not tend to perch at the minimum distance from each other, as indicated from the interaction distance and the distribution curve.

Hediger (1955) estimated the Barn Swallow's individual distance to be 15 cm, whereas I found it to be 12 to 13 cm. The Cliff Swallow's 10–11 cm individual distance and their large percentage of interactions where the aggressor retreated, correspond well with Emlen's (1952) observations.

Interactions where the aggressor remained were mostly restricted to the individual distance interval in the Cliff Swallow, but ranged more widely in the Barn Swallow. This and the Cliff Swallow's more prominent peak interval indicate greater rigidity of individual distance than for the Barn Swallow. Barn Swallow flocks and colonies are often smaller than those of the Cliff Swallow; individual recognition within a Barn Swallow flock would be more likely, resulting in more complex social relationships and more variable spatial patterns. Vocalizations of these species, with the Cliff Swallow's repertoire being smaller than that of the Barn Swallow (Samuel 1971), tend to confirm the Cliff Swallow's less complex social structure. Greater spatial homogeneity might also occur within pre-migratory Cliff Swallow flocks in correlation with increased flock integration.

Individual distance can be a sharp threshold as Grubb (1974) and I found, or a zone of intolerance as determined by Marler (1956) and Dilger (1960). These differences in individual distance values may be due to differences in experimental approach and the birds' activities. Marler and Dilger used 2 movable feeding hoppers to bring captive Chaffinches (Fringilla coelebs) and Common Redpolls (Acanthis flammea) respectively into close proximity. The perching swallows' major activities were resting and preening, as is likely for Grubb's perched Herring Gulls. McBride (1971) suggested that individual distance be measured at rest when it is constant; Crook (1961) reported that individual distance varies with food dispersion. Determination of individual distance may be more distinct and comparable for perched birds than for feeding birds.

Swallows often took advantage of another's preoccupation to approach closely—a phenomenon also recognized by Emlen (1952), Crook (1961), and McBride (1964). Such approaches always resulted in displacement of the incumbent, and unnoticed intruders pecked preoccupied birds, indicating the approaches were of aggressive intent rather than contact seeking behavior.

Inter- and intraspecific spacing in swallows may decrease, or contact be tolerated, during unusually cold weather (Grubb 1973, Meservey and Kraus 1976). During adverse weather it may be more advantageous to conserve energy by bodily contact than to maintain individual distance.

The toleration of young birds within the individual distance may be
adaptive for colonial life because of the close association of adults and young swallows.

SUMMARY

Field observations and still and motion pictures were used to analyze the spatial patterns of perched Barn and Cliff swallows in Chase County, Kansas from 23 June to 19 September 1975. Individual distance was determined from analysis of spatial interactions between approaching and incumbent birds.

Both species perched near the individual distance; both species had greater inter- than intraspecific spacing; and interspecifics did not tend to perch at the minimum approachable distance. A similarity of swallows' interaction distances and spatial behavior may help explain the apparent spatial regularity of mixed-species flocks. Individual distances of Barn and Cliff swallows differed significantly. The Cliff Swallow's individual distance appears to be more rigidly maintained, possibly because of a simpler social organization or increased integration of their pre-migratory flocks.

The maintenance of spacing was dependent on head orientation and attentiveness. Distances increased during preening activities, which lessened interference and potential conflicts between adjacent birds. Adults tolerated young birds and adults in a submissive posture within their individual distance.

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LITERATURE CITED


BOX 2, WILLAMSBURG, MO 63388. ACCEPTED 1 MAY 1977.
POPULATIONS OF BAY-BREASTED AND CAPE MAY WARBLERS DURING AN OUTBREAK OF THE SPRUCE BUDWORM

DOUGLASS H. MORSE

Densities of both the Bay-breasted Warbler (Dendroica castanea) and the Cape May Warbler (D. tigrina) are generally believed to undergo striking local increases during outbreaks of the spruce budworm (Choristoneura fumiferana Clem.), an important defoliator of northern coniferous forests (e.g., Kendeigh 1947, Hensley and Cope 1951, Stewart and Aldrich 1951, 1952, MacArthur 1958, Morris et al. 1958). However, none of the studies have combined censuses of the birds, measurements of the birds’ food supply (budworms), and descriptions of the detailed foraging patterns of the birds. I made observations on Bay-breasted and Cape May warblers during June 1976 in the Aroostook Valley, Aroostook and Penobscot counties, Maine, an area experiencing heavy defoliation by budworms during 1976 and the 2 preceding seasons. In particular I sought to document these birds’ foraging patterns, their population densities, and the densities of other Dendroica species during a period when it could be easily demonstrated that a superabundant source of food was available.

STUDY AREA AND METHODS

The study area was in northern Maine and centered about 46°23'N, 68°44'W; where Township 8, Range 8; Township 8, Range 7; (Penobscot Co.) and Township 9, Range 7; (Aroostook Co.) adjoin. This site is on the south bank of the Aroostook River where it is joined by Laponkeag Stream. I conducted most of the study within an area of 15 km², but carried out additional observations elsewhere within these 3 townships.

The study area consisted mostly of second-growth balsam firs (Abies balsamea) and red spruces (Picea rubens), with smaller numbers of quaking aspens (Populus tremuloides). These trees generally reached a maximum height of 18-24 m and for the most part had a rather open understory (Fig. 1a). This vegetation predominated in the lower, well-drained parts of the area, but on higher ground considerable numbers of deciduous trees (primarily red maple [Acer rubrum], sugar maple [A. saccharum], yellow birch [Betula lutea], and beech [Fagus grandifolia]) occurred as well as the firs and spruces (Fig. 1b). On low, poorly drained soil northern white cedars (Thuja occidentalis) occurred frequently among the other conifers. No pesticides had been applied to the areas where the study was carried out (D. A. Stark in litt.).

Methods used generally followed those of earlier studies (Morse 1958, 1976). Briefly, I measured the amount of time that given individuals spent foraging at different heights and parts of the trees (tip of foliage, inner part of the limbs, etc.). A maximum of 5 min of foraging was taken per individual (usually it was not possible to obtain this much information before a bird was lost). Since these data were seldom gathered in the
same area more than once, little if any duplication of individuals occurred. These observations were made upon males for the most part. Since many individuals were first located by their songs, it is possible that their foraging patterns at this time differed from the ones they usually used. However, when the data from the first minute of foraging were compared with those gathered subsequently, no significant difference appeared (p > 0.05 in a \( \chi^2 \) test), so all data were combined.

Densities of breeding birds were established in 2 study plots, both 3.3 ha in size. One area was primarily coniferous (88%), while the other contained a considerably higher proportion of deciduous growth (only 60% coniferous). Eight censuses were made in each area, each lasting for nearly an hour. Where individuals held territories at the edge of the plots, I counted the number of observations made inside and outside the study area and assigned the bird in question a fraction of total occupancy.

Earlier studies on *Dendroica* warblers (Morse 1976) showed no simple relationship between total insect biomass and population sizes of insectivorous birds, but did establish...
that these birds took lepidopteran larvae at a rate far in excess of these insects' abundance. Mitchell (1952) and Dowden et al. (1953) have demonstrated a heavy intake of budworms by Bay-breasted and Cape May warblers when those prey were abundant. For these reasons and because of the extremely high densities of budworms in the present study, I confined measurements of food to the numbers of budworms present. These included counts of larvae and pupae in the canopy. I could also locate a high percentage of the budworms in their webs on exposed branches by viewing from the ground with binoculars. These censuses provided a second measure of abundance.

RESULTS

Foraging observations.—Bay-breasted Warblers concentrated their activities at medium to medium-low heights upon dead limbs and the inner parts of live limbs with little if any foliage, though they also foraged regularly upon the peripheral parts of live limbs in the midst of the foliage (Fig. 2). However, they spent little time exploring the distal tips of the vegetation (Fig. 2). They foraged upon red spruces more frequently (52.0% of observations) than would be predicted judging from the composition of the forests (Table 1) ($p < 0.01$ in a $\chi^2$ test on the original observations). Cape May Warblers, on the other hand, concentrated their activities on the peripheral parts of the vegetation near the tops of the trees, though relatively little of their foraging time was spent upon the distal tips of the foliage (Fig. 2). They foraged even more heavily upon red spruces (71.2% of observations)
Table 1

Composition of Canopy Trees on Study Sites (Random Sample of 100 Trees)

<table>
<thead>
<tr>
<th>Habitat</th>
<th>% fir</th>
<th>% spruce</th>
<th>% other conifers</th>
<th>% deciduous</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primarily coniferous</td>
<td>54</td>
<td>34</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>Coniferous-deciduous</td>
<td>41</td>
<td>14</td>
<td>7</td>
<td>38</td>
</tr>
</tbody>
</table>

1 Cedar, hemlock.

than did Bay-breasted Warblers (p < 0.001). Thus, based upon foraging locations alone, the 2 species segregated their activities almost completely, even though they both favored red spruces.

Relatively few foraging maneuvers other than gleaning were noted. Bay-breasted Warblers were observed to hawk for insects twice and to hover at the tips of vegetation twice. Cape May Warblers were observed to hawk twice. Only a modest percentage of time was spent actively foraging. During

Table 2

Density of Small Passerine Birds on Study Site in Pairs/40 ha (100 Acres)

<table>
<thead>
<tr>
<th>Species</th>
<th>Site 1—primarily coniferous</th>
<th>Site 2—coniferous-deciduous</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wood Thrush (Hylocichla mustelina)</td>
<td>8</td>
<td>—</td>
</tr>
<tr>
<td>Hermit Thrush (Catharus guttatus)</td>
<td>11</td>
<td>—</td>
</tr>
<tr>
<td>Swainson’s Thrush (C. ustulatus)</td>
<td>29</td>
<td>28</td>
</tr>
<tr>
<td>Golden-crowned Kinglet (Regulus satrapa)</td>
<td>48</td>
<td>—</td>
</tr>
<tr>
<td>Ruby-crowned Kinglet (R. calendula)</td>
<td>12</td>
<td>—</td>
</tr>
<tr>
<td>Solitary Vireo (Vireo solitarius)</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>Red-eyed Vireo (V. olivaceus)</td>
<td>9</td>
<td>4</td>
</tr>
<tr>
<td>Northern Parula (Parula americana)</td>
<td>—</td>
<td>12</td>
</tr>
<tr>
<td>Magnolia Warbler (Dendroica magnolia)</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td>Cape May Warbler (D. tigrina)</td>
<td>12</td>
<td>1</td>
</tr>
<tr>
<td>Black-throated Blue Warbler (D. caerulescens)</td>
<td>—</td>
<td>41</td>
</tr>
<tr>
<td>Yellow-rumped Warbler (D. coronata)</td>
<td>12</td>
<td>—</td>
</tr>
<tr>
<td>Blackburnian Warbler (D. fusca)</td>
<td>12</td>
<td>35</td>
</tr>
<tr>
<td>Bay-breasted Warbler (D. castanea)</td>
<td>72</td>
<td>83</td>
</tr>
<tr>
<td>Ovenbird (Seiurus aurocapillus)</td>
<td>47</td>
<td>41</td>
</tr>
<tr>
<td>Rose-breasted Grosbeak (Pheucticus ludovicianus)</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>Purple Finch (Carpodacus purpureus)</td>
<td>—</td>
<td>7</td>
</tr>
<tr>
<td>Dark-eyed Junco (Junco hyemalis)</td>
<td>48</td>
<td>—</td>
</tr>
</tbody>
</table>

TOTAL 323 262
the process of gathering the foraging observations upon Bay-breasted Warblers (4181 sec), individuals showed no sign of foraging activity during an additional 6702 sec, either perching motionless or preening alternately between songs. Foraging thus constituted only 38.4% of the time during which males were observed. The ratio was even more extreme for Cape May Warblers. While 1362 sec of active foraging observations were made, 4139 sec of non-foraging activity were noted, with foraging in this case taking up but 24.8% of the time during which males were observed. Probably these figures are conservative in both cases, particularly for Cape May Warblers, since I frequently searched for considerable periods of time before locating singing birds. Most likely I did not sight them sooner because they were inactive.

Censuses.—Bay-breasted Warblers were common on both coniferous and mixed coniferous-deciduous census plots (Table 2). Contrary to expectation, however, concentrations were slightly higher on the mixed plot than on the coniferous plot. Cape May Warblers were much less common than Bay-breasted Warblers (Table 2). Furthermore, based upon these censuses and other observations, they were confined to low-lying areas composed primarily of tall red spruces and balsam firs. Only in one area visited did Cape May Warblers’ territories closely adjoin each other.

Several other species of insectivorous birds occupied the 2 plots (Table 2), including other Dendroica species, as well as members of additional warbler genera and other passerine families. Of the 18 species cumulatively nesting on the 2 areas, only 6 were found on both. In both places the Bay-breasted Warbler was the most abundant species present. Of tree-dwelling warblers (Dendroica and Parula), only 3 of 7 species nested on both study areas (Magnolia Warbler, Dendroica magnolia; Blackburnian Warbler, D. fusca; and Bay-breasted Warbler), and of these, only the Bay-breasted Warbler was common on both. Of the other 6 tree-dwelling species (kinglets, vireos, grosbeaks, finches), only the Red-eyed Vireo (Vireo olivaceus) occurred on both areas, and then only at low density. Two of the 5 primarily ground-dwelling species (thrushes, ovenbird, junco) occupied both areas, both in relatively similar high density (Swainson’s Thrush, Catharus ustulatus: Ovenbird, Seiurus aurocapillus). Therefore, Bay-breasted Warblers were among the few species, and were the only primarily arboreal species, that regularly nested in high density in both habitats.

Food supply.—I calculated budworm numbers in terms of individuals/branch. Virtually all branches inspected contained at least one budworm, and most branches in the crowns of trees contained several (Table 3). Using the estimated food demands of these warblers in the literature (George and Mitchell 1948, Mitchell 1952), one can calculate the approximate impact of
The birds upon the resource (Table 4) and whether this resource is likely to become limiting.

Even the maximum likely intake involves only a small part of the budworm population (Table 4). The actual intake probably falls nearer the minimum likely intake (Table 4). Thus, this single resource turns out to be sufficient to support the entire bird population several times over. These measurements thus suggest strongly that the birds have a superabundant food source, at least to the degree that they can survive solely upon this food source.

### Table 3
**Number of Budworms per Branch** on Study Sites (±1 s.d.)

<table>
<thead>
<tr>
<th>Study site</th>
<th>Fir</th>
<th>Spruce</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Larvae</td>
<td>Pupae</td>
</tr>
<tr>
<td>MANUALLY INSPECTED</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Primarily coniferous</td>
<td>3.3 ± 0.7</td>
<td>5.3 ± 0.9</td>
</tr>
<tr>
<td>VISUALLY INSPECTED</td>
<td>larvae and pupae</td>
<td>larvae and pupae</td>
</tr>
<tr>
<td>Primarily coniferous</td>
<td>4.0 ± 1.1</td>
<td></td>
</tr>
<tr>
<td>Coniferous-deciduous</td>
<td>5.6 ± 1.2</td>
<td></td>
</tr>
</tbody>
</table>

1. Based upon a total of 10 branches from 5 different trees.

### Table 4
**Numbers and Exploitation of Spruce Budworms**

<table>
<thead>
<tr>
<th></th>
<th>Site 1—primarily coniferous</th>
<th>Site 2—coniferous-deciduous</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spruce trees/ha</td>
<td>3722 ± 464.6</td>
<td>1260 ± 236.4</td>
</tr>
<tr>
<td>Fir trees/ha</td>
<td>2341 ± 292.4</td>
<td>430 ± 80.8</td>
</tr>
<tr>
<td>Branches/spruce tree</td>
<td>108 ± 10.4</td>
<td>-</td>
</tr>
<tr>
<td>Branches/fir tree</td>
<td>102 ± 10.1</td>
<td>-</td>
</tr>
<tr>
<td>Total budworms/ha</td>
<td>4,307,423</td>
<td>1,442,045(^1)</td>
</tr>
<tr>
<td>Estimate number of budworms removed per ha by birds(^2)</td>
<td>44,608–111,520</td>
<td>36,309–90,773</td>
</tr>
<tr>
<td>% of total budworms removed by birds</td>
<td>1.0–2.6</td>
<td>2.5–6.3</td>
</tr>
</tbody>
</table>

1. Based upon the assumption that the visual scanning technique resulted in an underestimate, from comparison of these results with hand-sorting techniques from Site 1 (Table 3) used in the calculation of budworm numbers for that area, I have multiplied the spruce data by 1.2 and the fir data by 1.4.

2. Maximum based upon estimate of 35,000 taken/acre/season by 2.5 pr./acre plus their young (George and Mitchell 1948). Minimum based upon 40% of the above, the volumetric proportion of budworms found in stomachs during a moderate infestation (Mitchell 1952).
DISCUSSION

Foraging.—The spatial placement of Bay-breasted and Cape May warblers relative to each other resembles that reported by MacArthur (1958). However, the foraging patterns of these Bay-breasted Warblers differed from those documented by MacArthur, in that individuals spent considerably more time on dead limbs, generally at a low height, than did MacArthur's birds. Initially, this type of behavior seems paradoxical for a bird that feeds heavily upon budworms, prey that, true to their name, concentrate primarily upon new growth. However, upon several occasions Bay-breasted Warblers were observed to capture budworms descending on their threads (probably locating new feeding sites, since this species typically pupates on the foliage; Morris and Miller 1954). Foraging upon dead limbs may thus be highly efficient for the bird; visibility is good because there is no foliage and the larvae are unable to retreat into their webs as they do when approached in the foliage. Put in this context, even remaining motionless in these locations may represent part of a highly effective feeding strategy on the part of Bay-breasted Warblers.

Since MacArthur (1958) did not report the density of lepidopteran larvae in his studies, it is impossible to account for the presently-noted discrepancy in foraging patterns of Bay-breasted Warblers in the 2 studies. However, the most likely explanation is that his birds were not experiencing high densities of budworms.

The foraging patterns of the Cape May Warblers, which concentrated on the distal (but not terminal) part of limbs high in the trees, would give them ready access to budworms. A considerable proportion of new growth on these coniferous limbs occurs on the tops of these branches.

Population density.—The densities of Bay-breasted and (particularly) Cape May warblers recorded in this study are lower than those reported in certain other studies in areas of budworm outbreaks (Kendeigh 1947, Hensley and Cope 1951, Stewart and Aldrich 1951, 1952), though higher than most (Erskine 1971, 1972, 1976). While numbers of Bay-breasted and Cape May warblers in this study exceeded those typical of non-outbreak situations (Sanders 1970, Erskine 1971, 1972, 1976), their density, plus that of the other Dendroica species in the 2 census plots, approximated those of the combined Dendroica species in coastal spruce forests not experiencing such an increase of insect numbers (Morse 1976). This evidence suggests that even at this high food density, part of the change in insectivorous bird populations results from a substitution of species. Such a shift is consistent with Morris et al.'s (1958) observations that densities of several other species of Dendroica warblers decreased when those of Bay-breasted Warblers
increased. On the other hand, Sanders (1970), censusing areas where Kendeigh (1947) had worked earlier, found that bird populations in the absence of a budworm outbreak were very similar to those found by Kendeigh, except for the nearly complete absence of the budworm specialists.

Food supply.—It seems highly unlikely that the numbers of budworms were limiting the size of the population of either the Bay-breasted or Cape May warblers; censuses of budworm densities indicated that they were present in large numbers (usually several per branch) in both study areas. At this density only a small percentage of these insects was eaten. Further, the warblers spent only a minority of their time actively foraging, which suggests that they could have gathered far more food items than they did, if demands had existed for them. Though most observations were made upon males, which in the case of several congeners typically forage more slowly than their females during this period (Morse 1968, Black 1975), the high abundance of food militates against time restrictions providing a severe problem even for the females.

Population limitation.—This study does not permit a definite answer to the question of what factors place a limit upon the density of these species when food becomes superabundant. Most likely, however, the answer will be one of the following, or a combination of them: (1) Numbers of birds are inadequate to populate the areas more densely. This possibility is consistent with reports by Kendeigh (1947), Hensley and Cope (1951), and Stewart and Aldrich (1951, 1952) of even higher densities of Bay-breasted warblers, Cape May Warblers, and overall bird populations in other budworm outbreaks.

(2) Budworms do not provide a complete diet for these birds. The data of Mitchell (1952), showing that in a somewhat lighter outbreak of budworms than the present one insectivorous birds (including the 2 species of warblers of particular concern here) consumed only about 40% budworms by weight, suggests that other foods may be important in the diets of these birds. On the other hand, since Mitchell’s data were taken from denser bird populations than those studied here, nutrition seems unlikely to be of primary importance in regulating numbers at these lower densities.

(3) Territorial behavior may be limiting numbers. These birds were observed to chase and attack each other during this study, and references to similar behavior may also be found in other studies where superabundant food supplies existed (Kendeigh 1947, Morris et al. 1958). While such behavioral patterns may not seem adaptive under these conditions, they may be highly adaptive when resources are not abundant. Again, however, since other populations denser than the present ones have been reported, aggressive be-
behavior cannot in its own right account completely for the population densities reported in this paper.

SUMMARY

The foraging patterns, food supply, and population density of Bay-breasted and Cape May warblers were studied during a budworm outbreak in the spruce-fir forests of northern Maine. Bay-breasted Warblers foraged more intensively on low dead limbs than previously reported, probably a result of searching for budworms descending on threads from higher in the canopy.

Cape May Warblers concentrated their activities in live vegetation near the tops of trees. Males spent no more than ¼ to ½ of their time foraging. Bay-breasted Warblers were the commonest species upon plots censused both in lowland spruce-fir forest and in upland forest containing up to 40% deciduous growth. Budworm numbers were far in excess of the food demands of these warblers or the insectivorous birds as a group.

ACKNOWLEDGMENTS

I thank J. H. Fellers and E. S. Morton for comments upon the manuscript. The North Maine Woods Organization permitted fieldwork to be conducted upon their lands. A. E. Brower recommended the study area.

LITERATURE CITED


AGE AND FORAGING ABILITY RELATIONSHIPS
OF OLIVACEOUS CORMORANTS

MICHAEL L. MORRISON, R. DOUGLAS SLACK, AND EDWIN SHANLEY, JR.

The gradual development of food capturing abilities by young birds has been documented in several species that exhibit marked differences in foraging methods and sites. The young of Brown Pelicans (Pelecanus occidentalis; Orians 1969), Little Blue Herons (Florida caerulea; Recher and Recher 1969), Sandwich Terns (Sterna sandvicensis; Dunn 1972), and Adelie Penguins (Pygoscelis adeliae; Ainley and Schlatter 1972) all capture prey less successfully than do adults of their species. Although immature Royal Terns (Sterna maxima) capture prey as successfully as adults, they must increase feeding time due to slower diving rates (Buckley and Buckley 1974).

Relative foraging inefficiency by immatures has been given as a primary reason for evolution of delayed breeding in birds. Lack (1954, 1966, 1968) and Ashmole (1963) developed the basic premise that an individual's chances of surviving and producing offspring increase by delaying first reproduction until some optimal time as determined by local conditions.

Most cormorants normally exhibit a 2 to 3 year delay in first breeding (Skutch 1953, Lack 1968). This delay may in part result from lower foraging efficiency by immature cormorants. However, no study of comparative foraging efficiency between cormorant age groups has been previously published.

Our study was initiated to determine relationships of age and foraging abilities in Olivaceous Cormorants (Phalacrocorax olivaceus; unless otherwise noted, all references to cormorants mean this species). We used 2 study sites to assess the effect of varying habitat characteristics on cormorant foraging abilities, and to determine if relative age group efficiency rates were similar between different habitats. Differences in relative foraging efficiency and diving abilities of adult and immature cormorants could affect survival rates, and on a broader scale, help explain the development of delayed maturity.

METHODS

Adult and immature (first-year) Olivaceous Cormorants are readily distinguished by plumage differences (Oberholser 1974). Both age groups spent the majority of a day on or adjacent to feeding grounds, using posts, pilings, and trees as perch sites between feeding sequences. We recorded the diving and surface pause times between dives, number of successful dives, duration of feeding sequence, water depth, and weather parameters (e.g., air temp., wind speed, precipitation) for each feeding observation. Either a coworker recorded these activities immediately or we tape-recorded and later
timed and transcribed the recordings. All observations were made using 20--45× spotting scopes and/or 7× binoculars from a parked vehicle. A successful dive was scored only when a bird surfaced with and swallowed a prey item (neither size nor species could be accurately determined). Although subsurface prey swallowing does not normally occur (Ross 1976), we assumed that any such activity occurred equally between age groups. Data analysis did not include any sequence of fewer than 10 dives, or one in which a bird was disturbed (e.g., other birds, aircraft, people).

On 10 occasions (5 each) between 19 June and 4 November 1976, we recorded data at 1 of 2 study sites of marked habitat differences. Sportsman’s Road Marsh (SRM), Galveston Island, Texas, was an estuarine area characterized by shallow (0.25 to 0.75 m), tidally influenced water levels. Low tide produced ponds of various sizes that trapped and concentrated prey. Clumps of Spartina were scattered throughout the area. Herons, egrets, and other marsh and shore birds also used SRM for feeding. In contrast, Cedar Bayou Spillway (CBS), near Baytown, Texas, was an approximately 50 ha power plant cooling pond. Water levels were held roughly constant and were consistently deeper (0.75 to 2.0 m) than water levels at SRM. The feeding area contained no emergent vegetation. Only several species of terns and gulls fed in the area with the cormorants. Adult and immature cormorants fed in the same areas within each site.

Average percent successful dives (% success), success rates (success/min), diving rates (dives/min), dive times, surface time between dives (pause time), and dive/pause ratios (D/P) were calculated for adults and immatures at each study site. Due to skewed distribution and presence of zero values, we normalized percent data ($\sqrt{x + \frac{1}{2}}$ transformation) following Steel and Torrie (1960) before analysis. Means of adult and immature foraging success and diving times were tested for significant inter- and intra-area differences using Student’s t-test. Simple linear correlation coefficients (r) were run for all success and diving variable calculations versus climatic variables, water depth, and time and date of occurrence. The Spearman Rank Coefficient (r$_s$) was used to determine the relationship between adult and immature success rates.

RESULTS AND DISCUSSION

Adult vs immature foraging efficiency.—Foraging success of adult cormorants was significantly higher than that of immatures; this difference was approximately the same between study sites (Table 1). Foraging techniques of cormorants are thus skills which must be developed through experience.

Immatures had apparently not acquired the foraging ability of adults as they entered their first winter as no increase in their relative efficiency was noted (Fig. 1). An influx of fledglings at various times into study populations may have partially masked minor efficiency gains by first young of the year. However, as most Texas cormorant colonies become inactive by July, the latter 4 months of this study were free of such new additions (as reflected in the last 5 data points on Fig. 1).

Although the relationship was weak ($r_s = 0.310$, t = n.s.), respective success rates of both age groups fluctuated in about the same degree between study dates. We noted no diurnal variation in success or frequency for either age group. Except for one occasion, as adult success increased or de-
Table 1

Inter- and Intra-area Comparisons of Adult (AD) and Immature (IMM) Olivaceous Cormorant Foraging Parameters

<table>
<thead>
<tr>
<th></th>
<th>Cedar Bayou (CBS)</th>
<th>Sportsman’s Road (SRM)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>IMM</td>
<td>AD</td>
</tr>
<tr>
<td>Success (%)</td>
<td>9.9*</td>
<td>17.7*</td>
</tr>
<tr>
<td>Success/Min</td>
<td>0.28*</td>
<td>0.55*</td>
</tr>
<tr>
<td>Dives/Min</td>
<td>2.76</td>
<td>2.84</td>
</tr>
<tr>
<td>Diving Time (Sec)</td>
<td>17.82</td>
<td>15.25</td>
</tr>
<tr>
<td>Pause Time (Sec)</td>
<td>5.49</td>
<td>5.48</td>
</tr>
<tr>
<td>Dive Pause (D/P)</td>
<td>3.31</td>
<td>2.74</td>
</tr>
<tr>
<td>Sample Size</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. Dives</td>
<td>338</td>
<td>435</td>
</tr>
<tr>
<td>No. Birds</td>
<td>25</td>
<td>32</td>
</tr>
</tbody>
</table>

*p < 0.05; all inter-area comparisons, except % success and D/P, were significant (p < .01).

Increased, immature success did likewise. A factor, or group of factors, may have affected foraging ability of both age groups similarly. All measured weather factors were relatively constant throughout this study, and did not correlate with any diving or success variable. Variations in prey availability

Fig. 1. Comparison of prey capture success (%) of adult and immature Olivaceous Cormorants (results from both study sites combined).
among study dates may have affected cormorant success. Dunn (1972) attributed a similar success rate pattern between adult and immature Sandwich Terns to variations in prey availability. Unfortunately, prey species and concentrations were not sampled during this study.

Immatures spent a greater proportion of a day feeding than adults. Although actual time spent in a single feeding sequence did not vary significantly, immatures returned to feed nearly twice as often as did adults (Table 2, data from SRM only; use of scattered roost sites allowed determination of an individual’s sequential activities at SRM, while use of a common roosting area prevented following an individual at CBS). Therefore, actual food intake per day may be roughly equal for both age groups. Under this assumption, immatures could obtain adequate food for maintenance provided weather conditions permitted an increase in foraging time as needed. This possibility was suggested for immature Little Blue Herons (Recher and Recher 1969) and Sandwich Terns (Dunn 1972) as a means of compensation for lower capture success.

Rate of adult prey capture (success/min) during a feeding sequence exceeded that of immatures at both study sites, though significantly so only at CBS (Table 1). The deeper, more open water at CBS may have accentuated immature inefficiency. Although not quantified, handling time (manipulation of prey prior to swallowing) and loss of captured prey appeared greater for immatures, further decreasing success (and thus, food intake). Success rate also followed the pattern as shown in Fig. 1.

Although their capture efficiency was lower, immatures have acquired the diving abilities of adults at, or soon after, fledging. Intra-area comparisons
of all diving variables were nearly identical for both age groups (Table 1). This suggests that immature foraging ineffectiveness was caused by a lack of subsurface abilities. The methods by which cormorants pursue, capture, and manipulate prey, along with the musculature associated with feeding, have been studied for adult Double-crested Cormorants (Phalacrocorax auritus) by Owre (1967). He felt that vigorous paddling of the feet and steering with the tail were necessary to overcome the difficulties of submerged swimming. Capture technique, maneuverability, and development of a prey search image may thus be gained through experience, and help account for greater foraging efficiency by adults.

Dive/pause (D/P) ratios have been used as an indicator of a species physiological diving abilities (Dow 1964). Similar D/P values for adults and immatures within and between sites is a further indication that both age groups possessed similar diving abilities. If dives and pauses of cormorants are interrelated, then this ratio should remain roughly constant for the species under normal conditions. D/P ratios for several cormorant species were determined (Table 3). Stonehouse (1967) felt that the mean D/P ratio may represent diving efficiency at the family level, while a high ratio for individuals probably represents physiological strain. He concluded that by working well within their physiological limit, cormorants may avoid exhaustion during prolonged fishing spells. Similarities in D/P ratios between various habitats and water depths suggest that the optimum diving rhythm among cormorant species is similar.

Habitat characteristics and foraging abilities.—Variations in habitat characteristics apparently accounted for marked diving rate differences between study sites (Table 1). The approximate 1 m average water depth difference between study sites was an important factor in cormorant diving ability. Significant correlations existed between water depth and all success and diving variables except % success (which does not reflect time spent in a feeding sequence; Table 4). Underwater visibility, substrate configuration, and water quality are other characteristics that vary among habitats and could also affect foraging abilities.

A further indication of inter-area success differences are number and length of daily foraging sequences. These variables were only measured at SRM (as previously discussed; see Table 2), but an indirect comparison between sites can be made. Capture rates were lower for both age groups at CBS relative to SRM, while % success was maintained between sites. This indicated that cormorants increased foraging time at CBS to compensate for lower capture rates. Water levels remained constant at CBS, while those at SRM were tidally influenced. Fish appeared to become trapped, and thus concentrated into small pools during low tide at SRM. Kushlan (1976)
<table>
<thead>
<tr>
<th>Species</th>
<th>No. Dives</th>
<th>Habitat (Depth, m)</th>
<th>Mean Dive (Sec)</th>
<th>Mean Pause (Sec)</th>
<th>D/P</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pelagic Cormorant (P. pelagicus)</td>
<td>44</td>
<td>Coastal (1.5–6.1)</td>
<td>45.3</td>
<td>23.2</td>
<td>2.0</td>
<td>Dow 1964</td>
</tr>
<tr>
<td>Pelagic Cormorant</td>
<td>20</td>
<td>N.A.</td>
<td>29.1</td>
<td>14.5</td>
<td>2.0</td>
<td>Dow 1964</td>
</tr>
<tr>
<td>Shag (P. aristotelis)</td>
<td>155</td>
<td>Pelagic (N.A.)</td>
<td>40.0</td>
<td>15.0</td>
<td>2.6</td>
<td>Lumsden &amp; Haddow 1946</td>
</tr>
<tr>
<td>Great Cormorant (P. carbo)</td>
<td>N.A.</td>
<td>Coastal Shallows (N.A.)</td>
<td>25.0</td>
<td>12.0</td>
<td>2.0</td>
<td>Van Dobben 1952</td>
</tr>
<tr>
<td>Great Cormorant</td>
<td>34</td>
<td>Coastal (avg. 10.7)</td>
<td>51.0</td>
<td>13.9</td>
<td>3.7</td>
<td>Ross (in press)</td>
</tr>
<tr>
<td>Double-crested Cormorant (P. auritus)</td>
<td>86</td>
<td>Coastal (avg. 4.7)</td>
<td>25.1</td>
<td>10.3</td>
<td>2.4</td>
<td>Ross (in press)</td>
</tr>
<tr>
<td>Olivaceous Cormorant(b) (P. olivaceus)</td>
<td>773</td>
<td>Cooling Pond (.75–2.0)</td>
<td>16.0</td>
<td>5.5</td>
<td>2.9</td>
<td>This Study</td>
</tr>
<tr>
<td>Olivaceous Cormorant(b)</td>
<td>1,348</td>
<td>Estuary (.25–.75)</td>
<td>6.3</td>
<td>3.0</td>
<td>2.1</td>
<td>This Study</td>
</tr>
</tbody>
</table>

\(b\) Adult and immature data combined due to similar results.
Table 4
Correlation Coefficients (r) for Water Depth vs 5 Diving and Foraging Success Variables of Olivaceous Cormorants

<table>
<thead>
<tr>
<th>Water Depth vs</th>
<th>Immatures</th>
<th>Adults</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dives/Min</td>
<td>-0.6088**</td>
<td>-0.7669**</td>
</tr>
<tr>
<td>Success/Min</td>
<td>-0.4905*</td>
<td>-0.4684*</td>
</tr>
<tr>
<td>Diving Time</td>
<td>0.6495**</td>
<td>0.6531**</td>
</tr>
<tr>
<td>Pause Time</td>
<td>0.5071**</td>
<td>0.4921**</td>
</tr>
<tr>
<td>Percent Success</td>
<td>-0.1538</td>
<td>-0.0987</td>
</tr>
</tbody>
</table>

* .001 < p < .01.
** p < .001.

found that the feeding efficiency of wading birds increases as water levels recede and fish become concentrated in remnant pools. It may take less time for cormorants to satisfy nutritional requirements at SRM as compared to CBS due to increased availability of prey as water levels fall.

**Mortality and life history strategies.**—Lower relative foraging efficiency among immatures may be a widespread occurrence in cormorants, as suggested by similar relative success values between sites in this study. The transition from nestling to independence in species whose food is sometimes hard to come by and whose feeding methods are skilled can be difficult (Ashmole and Tovar 1968). Development of prey capture abilities by immature cormorants is probably a strong selective force that eliminates all but the rapid learners.

It would follow that delayed reproduction in cormorants may be partially due to lack of foraging skills. Reproduction should be timed so that an individual can provide food for itself and young; reproductive rate and individual survival are thus maximized (Lack 1968, Recher and Recher 1969). Lowered physiological conditions and/or increased feeding times of immatures resulting from foraging difficulties could act to retard reproductive maturity until such foraging skills are fully developed. The exact length of delay (be it 2 or 3 years) could then vary depending upon a surviving individual's foraging abilities and localized breeding conditions (e.g., nest site and/or mate competition, weather variables, food supply). These views, as developed for numerous species by Lack (1954, 1966, 1968) and Ashmole (1963), have been widely adopted in explaining delayed maturity in several species whose immatures also exhibited foraging inefficiencies (Orians 1969, Recher and Recher 1969, and others).
SUMMARY

Relative foraging efficiency of adult and immature Olivaceous Cormorants was compared on 2 study sites in Texas. Foraging success of adults was higher than immatures, a difference that continued as immatures entered their first winter. Success for both age groups fluctuated in much the same pattern among study dates, and may have been due to prey availability. Immatures increased daily food intake by returning to feed twice as often as adults. Immatures acquired the diving ability of adults soon after fledging. Lower capture success by immatures may be caused by relatively poor capture techniques, maneuverability, and prey search image. Similarities in dive/pause ratio among cormorant species may be related to similarities in the diving abilities of the group.

Diving rate differences between study sites were likely due to variations in habitat characteristics. Significant correlations existed between water depth and all diving variables except % success. Foraging site selection is important to cormorant hunting success. Foraging time apparently increased to compensate for lower capture rates in areas of poor prey availability.

Immature mortality is likely increased during the transition from fledgling to adulthood due to foraging difficulties. Lowered physiological conditions and/or increased feeding times of immatures resulting from poor feeding success may partially explain delayed attainment of reproductive maturity for several years in cormorants.

ACKNOWLEDGMENTS

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LITERATURE CITED


ANALYSIS OF ROOSTING COUNTS AS AN INDEX TO WOOD DUCK POPULATION SIZE

Delbert E. Parr and M. Douglas Scott

Autumn roosting habits of Wood Ducks (Aix sponsa) have been studied throughout much of their range (Hester and Quay 1961, Hester 1965, Hartowicz 1965, Hein and Haugen 1966, Tabberer et al. 1971), but the use of roosting flight counts as a population index is controversial. An Iowa study (Hein 1965, Hein and Haugen 1966), concluded that fall roosting flight counts could furnish an index which would detect changes of 15% in annual abundance of Wood Ducks. In contrast, Tabberer et al. (1971) studied 44 roosts in Louisiana and concluded that flight counts were invalid due to variations in quality and stability of individual roosts. Smith (1958), in his study of roosts in Louisiana, felt that the technique was invalid because of yearly fluctuations in the amount of surface water in roosts.

If a roost count is to be a valid index technique, the following assumptions must be met (also see Hein and Haugen 1966): 1. Each roost is a geographically discrete area, which contains an identifiable Wood Duck population separate from other roosts. 2. The number of Wood Ducks using a roost reflects the general abundance of the species in the area, and the Wood Ducks congregate at the roost solely as a result of their social needs, not due to a presence, or absence, of food or water elsewhere. 3. All, or at least a consistent proportion, of the Wood Ducks flying to a roost are susceptible to being counted during any given counting event. 4. All, or at least a consistent proportion, of the Wood Ducks in an area fly to identifiable communal roosts in the evening. 5. Little unilateral inter-roost movement occurs.

We gathered and analyzed movement data on individual ducks, as well as on whole flocks to determine if these assumptions were valid for roosting Wood Ducks in southern Illinois.

STUDY AREAS AND METHODS

Three study areas were used (Fig. 1). The 2960 ha Union County Wildlife Refuge is located on the Mississippi River floodplain approximately 13 km west of the town of Anna. It contains 3 open-water lakes, plus several areas of standing timber which are artificially flooded in the fall. There are also scattered swampy areas in which buttonbush (Cephalanthus occidentalis) is the principal species. Uplands are composed of grain fields interspersed with oak (Quercus spp.)—hickory (Carya spp.) forest.

The 770 ha LaRue-Pine Hills Ecological Area is located approximately 14 km north of the Union County Refuge. The area is a swamp dominated by buttonbush, water willow (Decodon verticillatus) and American lotus (Nelumbo lutea). It has previously been described by the U.S. Forest Service (1970).
Fig. 1. Location of the 3 southern Illinois study areas and the 4 Wood Duck roosts. (1) North Pine Hills Roost; (2) South Pine Hills Roost; (3) Grassy Lake Roost; and (4) Triangle Roost.

The 1215 ha Oakwood Bottoms Greentree Reservoir is located in Jackson County, approximately 24 km north of the Union County Refuge. The dominant plants are pin oaks (Quercus palustris), which are flooded in the fall for waterfowl management purposes. Further description of this area is provided by Thomson (1971).
Roost locations and counts.—Wood Duck roosts were located by following flocks of birds in flight during the evening, as described by Hein and Haugen (1966). Once a roost was found, the number of birds using it was periodically counted to determine fluctuations in usage rate.

Incoming birds were counted from a place where they could be seen crossing open fields or water adjacent to the roost. At times, accurate counts could only be made from a boat. Counts were always made by 2 experienced observers to minimize overlooking ducks on large roosts. Counts at each roost were made once or twice a week from 20 August to 30 November 1973.

Counting always started at least 1 hour before sunset, in an attempt to determine when the first bird came to roost. The last bird was assumed to have arrived after a 10-min period passed during which no more birds were seen. A Weston Master V Universal exposure meter was used to measure light intensity when the first and last birds came to roost, so that possible poor sighting conditions could be quantified.

Trapping and marking.—Wood Ducks were captured between 11 and 26 September 1973, at a permanent site waterfowl trap baited with corn, as described by Arthur and Kennedy (1972). The trap was located midway between two Wood Duck roosting sites at Union County Refuge. All 961 trapped Wood Ducks were banded with U.S. Fish and Wildlife Service leg bands so that information on movements from hunter returns might be obtained. All banded Wood Ducks were sexed and aged by plumage (Carney 1964), eye color (Kortwright 1942:221), or cloacal examination (Hochbaum 1942).

Ten banded Wood Ducks were fitted with radiotransmitter packages, so that detailed analyses of their movements could be made. Radio packages weighed approximately 20 g. Transmitters operated in the 148-149 MHz frequency range and were a modification of the type described by Cochran (1967). The radio package, mounted on the back of the duck, was attached by a harness as described by Sanderson and Schultz (1973).

Instrumented birds were located by using a battery-powered 12-channel portable tracking receiver. It was equipped with a 3-element directional hand-held yagi antenna; an 8-element yagi antenna was mounted on a vehicle for mobile reception. Once, after 4 instrumented birds left the Union County Refuge, a light aircraft (Cessna 206), with the 3-element yagi antenna mounted on 1 of the landing gear struts, was used to locate the birds.

The location of instrumented Wood Ducks was determined by direct observation, or by triangulation, as described by Heezen and Tester (1967). The birds were located approximately 4 times per week in the evening after they went to roost. They also were radio-located at 2-h intervals during several diel (24-h) tracking periods to further determine roosting habits.

To insure that movements of Wood Ducks were not affected by radio packages, they were allowed to carry them for a short acclimation period before data were gathered. The birds were fitted with radio packages on 24 and 26 September 1973, and were then released at the trap site between the roosts on Union County Refuge. The trap was approximately 2.5 km from each roost. When released, the ducks remained on the lake from 1 to 14 days, with most moving to a roost within 4 to 5 days. Once a bird flew to a roost, its movements were no longer assumed to be influenced by the radio package.

RESULTS

Factors influencing roost counts.—Four roosts were located (Fig. 1). Two roosts—“Triangle” and “Grassy Lake”—were found on the Union County
Refuge, and the other 2, called "northern" and "southern," were located at the LaRue-Pine Hills Ecological Area.

Twenty-five evening roosting flight counts were made at the Triangle Roost from 20 August to 30 November 1973. The peak count of 2100 Wood Ducks was made on 21 September 1973. On the last count, 30 November, numbers had dwindled to nearly zero. At the Grassy Lake Roost, 7 counts were made from 2 September to 14 October 1973, after which it became impossible to make any more accurate counts due to the large number of other species of waterfowl flying to the roost. The peak count of 1500 Wood Ducks was made at this roost on 23 September 1973. Figures 2 and 3 show the trends and variability in these roosting flight counts. The late September peak and subsequent decline coincide with the results reported by Hein and Haugen (1966), but the counts showed highly irregular fluctuations similar to Hartowicz's (1965) results in southeast Missouri. For example, the decline in the Triangle Roost count on 20 September could not be explained by any environmental change. Triangle Roost counts did not show a significant correlation with changes in temperature \( r = .37, p > 0.05 \), but were slightly positively correlated with decreasing day length \( r = .50, p < 0.05 \), using the Pearson correlation coefficient (Snedecor and Cochran 1967:172).

Using the SPSS multiple-regression computer program (Nie et al. 1970) no significant relationship \( p > 0.01 \) was revealed between the numbers of birds counted and any combination of the daily parameters of temperature, day length, light intensity when the first bird arrived at the roost, or \% of the birds arriving before sunset (the number of counts on the Grassy Lake Roost was too small to be analyzed this way). Hein (1961 and 1965) also found no single climatic factor correlated with changes in numbers in roosting flights. Likewise, Tabberer et al. (1971) found that temperature, wind velocity, barometric pressure, and relative humidity had no effect on the number of ducks observed during roosting flight counts.

One cause of the fluctuations in counts at the Grassy Lake Roost was that many birds were missed on some evenings because the area was too large (200 ha) for 2 observers to see all incoming ducks. However, 2 definite concentrations of birds could not consistently be found on the lake, so the area was classified as 1 roost only.

Another factor influencing these roost counts was baiting at the trap site, even though the trap was 2.5 km from both roosts. As shown in Fig. 2, counts at the roosts dropped dramatically in late September, which coincided closely with a halt in baiting on 26 September. Also, prior to and after baiting, very few Wood Ducks entered either roost from the direction of the trap, but during the period of baiting, most of the flight to both roosts was from that direction. When the Illinois hunting season opened (after trapping
stopped), 19 ducks banded at the Union County Refuge (which included 2 instrumented birds) were recovered in the Oakwood Bottoms Greentree Reservoir feeding area (24 km north) and the LaRue-Pine Hills Ecological Area (14 km north). Since the 2 instrumented ducks (G and I) that originally fed and roosted at the Union County Refuge were known from tracking to have shifted their roost to the LaRue-Pine Hills Ecological Area and their feeding grounds to Oakwood Bottoms, it is likely that many of the other 17 refuge-banded birds that were recovered at Oakwood Bottoms and Pine Hills also were roosting at the LaRue-Pine Hills Ecological Area. These data indicate, then, that many birds that were feeding, and probably roosting, at the Union County Refuge moved to a new feeding area and roost when trapping stopped. Either this occurred, or these birds originally fed at the Union County Refuge trap site, and then flew past local roosts to reach the more distant Pine Hills roosts, which was not probable.

The use of Wood Duck roosts by large numbers of other waterfowl also caused counting problems in that rapidly flying birds could not always be differentiated as to species. The roosts on Union County Refuge were used
by Mallards (*Anas platyrhynchos*), Black Ducks (*Anas rubripes*), Green-winged Teal (*Anas crecca*), Blue-winged Teal (*Anas discors*), American Wigeon (*Anas americana*) and Canada Geese (*Branta canadensis*), as each migrated into the area. All of these species used the Triangle Roost during the day, but only Blue-winged and Green-winged teal came to this roost in significant numbers during the evening roosting flight. At the Grassy Lake Roost, however, Wood Duck counts were badly hampered by large numbers of Mallards, Black Ducks, American Wigeon, Green-winged Teal, and Canada Geese flocking to the area in the evening. The last attempt to make a count at the Grassy Lake Roost was on 18 October, when it proved impossible due to the large number of species using the roost.

Lighting conditions sometimes appeared to interfere with counting ducks, so light intensity readings were taken when the first and last birds in the evening roosting flight arrived. During these episodes, Wood Ducks were much more difficult to see in the dull light of cloudy days, particularly if they were not observed against a sky background. The increasing difficulty, though, was mainly due to the difference in the quality of the light and not the level of light intensity, since this remained at about 5 footcandles for the latest birds whether it was a clear or cloudy day.

Initial radiotracking indicated that some Wood Ducks were flying to the roost throughout the day. Consequently, Wood Duck activity was monitored at 2-h intervals during diel tracking periods to determine when birds were moving to and from roosting areas. The activity data indicated that Wood Ducks did not always return at the usual time of the evening roosting flight. Instrumented birds were observed flying to the roost both before the count was initiated and after it was completed. Ducks B, C, and E at least once each returned 3 to 6 h before counting began. Duck A once flew to the roost from its diurnal habitat during the night.

The direction from which a Wood Duck approached a roost in the evening also affected whether or not it could be counted. This was particularly apparent at the large Grassy Lake Roost where it was possible for a Wood Duck to fly unobserved to the roost if it did not return by commonly used flight lanes. An example of this is shown in Fig. 3, where an instrumented bird flew to the roost from the southeast through trees, rather than across open water as most roosting birds did and, therefore, would have been missed in the count.

Monitoring of the daily activity of Wood Ducks also revealed that some birds did not fly back to a communal roost every evening. One reason for this was that some birds continued to use the same swamp during the daytime. Instrumented Wood Ducks failed to leave the site during the day a total of 25 out of 46 diel tracking periods, or 54% of the time. An observer moving
Fig. 3. Diel movements of Duck B on 11–12 November 1973. Times (CST) of locations were: (1) 17:50 11 November; (2) 05:30 12 November; (3) 07:30, 09:30 and 11:30 12 November; (4) 13:30 and 15:30 12 November; and (5) 17:30 12 November. Sunrise was at 06:42. Sunset was at 16:47. Stationary nighttime locations not included.

through a roosting swamp could flush Wood Ducks all day long. This continuous use also has been reported by Hankla and Smith (1963), who noted that, at least in the South, roosts appeared to be used for daytime feeding.

Other Wood Ducks failed to return to their roosts once they left in the morning. This did not occur until the last 3 weeks of November, which was just prior to the roosts being abandoned as the birds moved south. At this time, some Wood Ducks were observed going to roost in other areas close to, but not in, the Triangle Roost, and instrumented birds occasionally failed to return from their diurnal habitat to the roost. On 3 occasions Duck A, and once Duck F, failed to return to the roost from the area in which they were feeding during the day. In another instance, Duck A returned to the roost vicinity just after sunset from an unknown location. Instead of going to the usual roost site, however, the bird roosted in nearby flooded timber.
A final factor that could have caused unreliable roost counts was the movement of Wood Ducks from one roost to another. The frequency with which Wood Ducks used the same roost was determined by locating instrumented birds after the evening roosting flight. Individual birds were located on the same roost 97% of the time (N = 295 observations), with ducks G and I the only birds displaying inter-roost movement. Duck G moved from the Triangle Roost to the Grassy Lake Roost and then to the northern roost at LaRue-Pine Hills Ecological Area. Duck I moved from the Grassy Lake Roost to the northern roost at LaRue-Pine Hills Ecological Area.

To determine the overall frequency and consistency with which the individual instrumented birds exposed themselves to a count at their usual roost, they were located prior to the evening roosting flight and then again during the flight or immediately following it. The results, summarized in Table 1, show that the weighted mean for all birds exposed to a count was 41% (± 31%, p < 0.05—confidence limits from the method of Snedecor and Cochran 1967:210). Counting exposure data were further analyzed to determine if instrumented birds as a group showed any environmentally-related trend in exposing themselves to a count. For each of the 17 days in which at least 4 birds were located before and after the roosting flight, the percent exposed to a count on that day was calculated. As indicated in Fig. 4, there was no apparent trend with season. Multiple linear regression analyses

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**Table 1**

Percent of the Days Individual Wood Ducks were Exposed to a Roosting Flight Count*

<table>
<thead>
<tr>
<th>Wood Duck I.D. code</th>
<th>No. days calculated</th>
<th>No. days exposed</th>
<th>% time exposed to counting</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>15</td>
<td>4</td>
<td>27</td>
</tr>
<tr>
<td>B</td>
<td>16</td>
<td>8</td>
<td>50</td>
</tr>
<tr>
<td>C</td>
<td>13</td>
<td>9</td>
<td>69</td>
</tr>
<tr>
<td>D</td>
<td>20</td>
<td>12</td>
<td>60</td>
</tr>
<tr>
<td>E</td>
<td>10</td>
<td>7</td>
<td>70</td>
</tr>
<tr>
<td>F</td>
<td>21</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>G</td>
<td>2</td>
<td>2</td>
<td>100</td>
</tr>
<tr>
<td>H</td>
<td>7</td>
<td>1</td>
<td>14</td>
</tr>
<tr>
<td>I</td>
<td>2</td>
<td>2</td>
<td>100</td>
</tr>
<tr>
<td>J</td>
<td>10</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>116</td>
<td>47</td>
<td></td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td>11.6</td>
<td>4.7</td>
<td>50</td>
</tr>
<tr>
<td><strong>Weighted mean</strong></td>
<td></td>
<td></td>
<td>41</td>
</tr>
</tbody>
</table>

*The number of days used in the calculation was the number of days individual birds could be located before and after a roosting flight count would have been made.
Fig. 4. Percentage of instrumented Wood Ducks exposed to evening roosting flight counts on individual days. Only those days when 4 or more birds could be located before and after the roosting flight were used. Numerals in parentheses equal the number of birds located that day.

revealed no relationship (p > 0.01) between the % exposed to a count and daily maximum, minimum, and mean temperature, day length, or number of birds being counted. The weighted mean % of all birds exposed for any given day was 37% (± 24%, p < 0.05). Not leaving the roost during the day
Table 2

Summary of Instrumented Birds' Failure to Meet Assumptions Necessary for Roost Counts to Provide an Accurate Census of Wood Ducks*

<table>
<thead>
<tr>
<th>Assumption</th>
<th>Number of times failed (69/116)</th>
<th>Percent of total failures (69)</th>
<th>Percent of total (116)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Roosts are geographically discrete.</td>
<td>3</td>
<td>4.3</td>
<td>2.6</td>
</tr>
<tr>
<td>2. Roost count is not affected by surrounding food or water.</td>
<td>Unknown number</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. All birds flying to a roost are susceptible to counts at a normal time.</td>
<td>Unknown number</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3A. No confusion due to other waterfowl.</td>
<td>Unknown number</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3B. Lighting conditions are suitable.</td>
<td>Unknown number</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3C. Birds fly to roost during counting interval.</td>
<td>5</td>
<td>7.2</td>
<td>4.3</td>
</tr>
<tr>
<td>3D. Birds approach roost from a visible direction.</td>
<td>3</td>
<td>4.3</td>
<td>2.6</td>
</tr>
<tr>
<td><strong>SUBTOTAL</strong></td>
<td>8</td>
<td>11.5</td>
<td>6.9</td>
</tr>
<tr>
<td>4. All birds fly to a communal roost on a given day.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4A. All birds leave roost during the day.</td>
<td>54</td>
<td>78.3</td>
<td>46.6</td>
</tr>
<tr>
<td>4B. All birds return to roost at night.</td>
<td>4</td>
<td>5.8</td>
<td>3.4</td>
</tr>
<tr>
<td><strong>SUBTOTAL</strong></td>
<td>58</td>
<td>84.1</td>
<td>50.0</td>
</tr>
<tr>
<td>5. No inter-roost movement.</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td>69</td>
<td>99.9</td>
<td>59.5</td>
</tr>
</tbody>
</table>

*Observations were made on 116 roosting flights by individual instrumented birds.

was the most common reason for Wood Ducks not being exposed to a count. Table 2 summarizes the relative importance of the other reasons why Wood Ducks would have been missed in roosting flight counts.

The number of counts necessary to obtain an accurate estimate of the size of a roosting population was calculated based upon the day-to-day variation in movements of the 10 individual instrumented birds as well as the group as a whole. The number of counts necessary was determined using the technique given by Snedecor and Cochran (1967:58). Using the sample variance of the mean (Snedecor and Cochran 1967:44) of individual birds being exposed to a count (weighted mean equals 41%) as an estimator of the population variance, 22 roost counts would be necessary for 15% accuracy at the 95% confidence level. Using the variance in the total percentage of instrumented birds exposed on a single day (weighted mean equals 37%),
15 counts would be necessary for accuracy within 15% at the 95% confidence level.

**DISCUSSION**

The changes in Wood Duck roosting flight counts in this study (Figs. 2 and 3) corresponded with those reported by Hein and Haugen (1966). Hein (1961) felt the September peak in numbers was due to this being the time when most adults and juveniles were capable of flight. The decline in the roosting flight count after the September peak was thought to be due to dispersal of birds in all directions (Stewart 1958). The movement of 19 banded and instrumented birds 14 km north of the banding site in this study tended to verify the dispersal concept. This is further supported by Brown (1972) who found, through band and tag returns, that there was a late summer dispersal of adult and juvenile male Wood Ducks as far north as Wisconsin from Arkansas. The smaller October peaks in counts in this study probably were due to new migrants moving into the area, as Hein and Haugen (1966) concluded in Iowa.

Although the counts of roosting Wood Ducks in southern Illinois followed the general trends found in other studies, all of our 5 previously described requisites for a roost count to be a valid indexing technique were not met throughout the autumn. Results of this study, in relation to the 5 assumptions, were:

1. All roosts were not geographically discrete, as revealed by the problems in identifying the roosts at the large Grassy Lake Roost area. Hein and Haugen (1966:660) noted that a large Iowa roost had “three foci within slightly less than 1 square mile,” and that “at some marshes, Wood Ducks used several roosting sites.” This indicates that large, indistinct roosts are not unique to southern Illinois.

2. The presence of a food supply apparently can affect the number of birds flying to local roosts, as was shown by the change in the direction of roosting flights when bait was present at a trap site and by the movement of birds from the trap to the Oakwood Bottoms Greentree Reservoir where acorns were becoming available as a new source of food. The numbers of Wood Ducks flying to roosts also are evidently affected by the existing water conditions. Roosts were abandoned when they went dry (Smith 1958, Hein and Haugen 1966), and Tabberer et al. (1971) found that as surface water increased, the numbers of ducks observed during roosting flights decreased.

3. There were 4 reasons why Wood Ducks that flew to a roost were sometimes not susceptible to being counted. One reason was that the common use of roosts by several other species of waterfowl caused problems in
identifying and counting Wood Ducks. This was in contrast to a report by Hein and Haugen (1966), who stated that the Blue-Winged Teal was the only species found using Wood Duck roosts, and that this was infrequent in Iowa. Second, poor lighting conditions due to cloudy weather interfered with counting ducks. A third factor that limited susceptibility of flying Wood Ducks to being counted was that some birds flew to the roost either before or after the time in the evening when a roost count would normally be made. The only way this problem could be avoided would be for an observer to stay at the roost all day. Also, some of the birds flying to the roost early did not remain there, so the observer would have to continuously count birds leaving, as well as entering, the roost. The fourth factor causing some birds flying to the roost to be missed in a count was that birds occasionally approached the roost from a direction that prevented them from being seen. This could be a serious problem in an area where the direction of flight to available local food supplies might be changed from day to day.

4. Our fourth major assumption, that all of the Wood Ducks in an area fly to a roost in the evening, also was proved false. Some birds did not leave the roost on some days, and others failed to return some evenings. The failure of birds to leave the roost was the major cause for this assumption to be violated more than any of the other 4. Birds failed to return to the roost in the evening only late in the study (November) and, if roosting counts were made between 15 and 30 September, this part of the problem would have been avoided.

5. The last requisite, an absence of unilateral inter-roost movement, was essentially met. Instrumented birds were located on their primary roost 97% of the time.

The overall effect of the failure of most of these assumptions to be met on a consistent basis was that individual instrumented birds exposed themselves to a count on an average of only 41 (± 31) % of the days they were observed, while the average number of all instrumented birds exposed to a count on any given day was 37 (± 24) %.

Hein and Haugen (1966), from their study of roosts on the upper Mississippi River in Iowa, concluded that 50% or greater of the roosts in an area must be counted to detect changes of 15% in annual abundance of Wood Ducks. They also stated that, with a sample size of 25 roosts, and assuming a 95% confidence level, the maximum precision in average roosting flight counts per roost was about 3% in 2 successive falls. However, data from this study indicated that, due to the variation in counting exposure among individual birds and different days, 15 to 22 roosting flight counts must be made for accuracy within 15% at the 95% confidence level. Therefore, assuming this variance would be as great for a large number of birds, such
as seen in a roost count, and that all roosts were counted on the same day, the smallest area to which the index could be applied would be the area enclosing 15 to 22 roosts. This area could be reduced by counting some roosts more than once on different days, but this would cause an extension of the time required, which would be undesirable due to the constant change in roosting numbers with time as shown in Figs. 2 and 3. Realistically, chances of most researchers being able to economically synchronize 15 to 22 counts within a 2- or 3-day period appear to be small.

The high amount of individual and daily variability seen in the counting susceptibility of instrumented birds provided a quantitative basis for suspecting the accuracy of day-to-day roost counts. Additional observed variables that were not quantified, such as seasonal food and water availability, counting confusion due to the presence of other waterfowl, and poor sighting conditions, could cause daily and seasonal counting errors to be even higher.

A final unknown variable which might affect local counts of Wood Ducks is unusually early cold weather forcing additional migrants into an area, causing a local inflation of counts in southern areas and a decrease at northern roosts. What makes this factor particularly troublesome is that a change at one roost would probably have a corresponding opposite effect on other roosting areas, since ducks are highly mobile. The result is that an index in one location may be representing conditions over a larger, completely unknown geographic area. Counting errors such as this would be unknown to the biologist unless roost counts were made simultaneously throughout the flyway; this is not yet practicable.

SUMMARY

Wood Ducks were equipped with radio packages, and their roosting flights were observed throughout the fall to determine the validity of using flight counts as a Wood Duck population index. Seasonal trends in the numbers of ducks flying to roosts were similar to the results of other workers, but the trends could not be related to environmental factors such as temperature, day length, or light intensity. Evening roosting flight counts did not provide a valid index to Wood Duck population size for several reasons: (a) roosts were not always geographically discrete; (b) a changing food supply location caused the number of Wood Ducks flying to a roost to vary; (c) all birds that flew to a roost were not susceptible to being counted, because of confusion due to the presence of other waterfowl, poor lighting resulting from cloudy weather, birds not flying to the roost during the counting interval, or birds approaching the roost from a direction which offered poor counting visibility; (d) some birds did not fly to a communal roost on certain days, either because they never left the roost, or because they roosted alone elsewhere. Most ducks did, however, show high fidelity to their traditional roosts. The variability in the exposure of instrumented Wood Ducks to counting could not be related to temperature, day length, or the total number of birds being counted. As a result of this variability, 15 to 22 roost counts would have to be conducted simultaneously in an area for 15%
accuracy at the 95% confidence level. We do not feel that this counting intensity is practical.

ACKNOWLEDGMENTS

We are indebted to David Kennedy, Staff Waterfowl Biologist, Illinois Department of Conservation, for his assistance in conducting this study. We are grateful to Karen Crites, Robert Hileman, Fred Roetker, and Vic Hammer for their help in the field. We would like to thank Mike Sweet for supplying information on banded Wood Ducks killed in Oakwood Bottoms Greentree Reservoir, and we thank W. D. Klinstra, Cooperative Wildlife Research Laboratory, Southern Illinois University, for providing radiotelemetry receiving equipment. We thank Joe Newcomb, District Ranger, U. S. Forest Service for allowing access to U. S. Forest Service lands. The Max McGraw Wildlife Foundation and the Illinois Department of Conservation financed part of this study. We appreciate the financial support of Amax Coal Company in paying publication costs for this article.

LITERATURE CITED


GENERAL NOTES

Black Skimmer abundance on the Louisiana–Mississippi–Alabama coast.—This note reports on a coast-wide inventory of Black Skimmer (Rynchops niger) nesting colonies from Sabine Pass (Texas–Louisiana border) to the eastern shore of Mobile Bay, Alabama, conducted during the 1976 breeding season.

We searched all brackish and saline marshes, mainland beaches, and barrier islands of the study area at 4-week intervals in May, June, and July 1976, using both rotary- and fixed-wing aircraft, and found 37 Black Skimmer colonies (Fig. 1). Nesting aggregations less than 1 km apart were lumped as single colonies.

I obtained estimates of breeding adults on each colony using both aerial photography and active nest counts. I photographed nesting aggregations through the open side window of aircraft approximately 100 m above the colony using a hand held 35-mm camera with a 55-mm lens and fine grain black and white film. Photography was timed to coincide with a seasonal peak in incubation, which I observed to occur in late June and early July. Because most adult feeding was observed in the early morning and late afternoon, I photographed colonies at midday to include most breeding adults.

Individual birds within the nesting area were conspicuous against the light-colored sand or shell substrate and were separable from adults in adjacent loafering areas on subsequently developed prints. (Loafering adults were more densely spaced than nesters and usually stood below the beach berm.) Only adults in nesting areas were included in aerial photographic counts of breeding adults. To avoid duplicating counts, I pin-pricked each individual bird as it was counted on a photograph.

On the same day as aerial photography, we conducted a ground count of all “active” (i.e., containing eggs or young) nest scrapes. Empty scrapes were not counted because we could not be sure these represented currently active nest attempts. Three observers positioned about 5 m apart walked through a nesting area simultaneously following the same compass bearing. Each person counted all active scrapes on one side between himself and the next person (or between himself and the colony edge if his was the first or last transect). Our progress through the colony was marked by our footprints left in damp sand, so areas were not omitted or covered more than once.

By equating an active nest with the current breeding effort of one pair of birds, I doubled nest counts to convert to breeding bird counts and compared these bird counts with those obtained from aerial photographs of the same colonies on the same date. I selected the larger of the 2 bird counts as more representative of breeding adults active on a colony (Table 1). Our nest counts omitted incipient nesting attempts, i.e., empty scrapes and patches of beach defended by potential breeders. The photographic bird count, an instantaneous record of adults present, probably included most current and potential breeders but was affected by weather, feeding conditions, and the timing of photography relative to peak breeding at a given colony. Thus, both nest and bird counts were probably underestimates of current breeding abundance.

However, I found a strong correlation between bird counts and total nest counts ($r = .89, 2.2$ birds per nest) at skimmer colonies during incubation. Therefore, despite the problem of underestimation, either the bird or nest count did at least provide a representative index of abundance during the annual peak in incubation. I preferred the aerial photographic bird count because it was less disturbing to birds than ground censuses.
I counted 29,980 breeding adult skimmers in 37 colonies within the study area between 26 June and 15 July 1976. There were 19,205 adults on barrier beaches, 4982 on spoil islands, and 5793 on shell berms in the salt marshes. I observed greatest regional abundance on the barrier beaches from the Isles Dernieres to Barataria Bay, although large groups also nested on the southern Chandeleur island chain, and on spoils at the Mississippi River mouth.

Historic accounts of skimmer abundance on the north Gulf Coast are scarce. The intensity of search and census efforts was never adequately described, and place names mentioned in old reports are now difficult to locate on the highly dynamic Louisiana coastline; however, some comparisons can be drawn between historic and current abundance in certain regions and at a few specific colony sites.

I could find no mention of skimmer nesting from Sabine Lake to Atchafalaya Bay before 1940. Small colonies (fewer than 300 adults) were reported at Calcasieu Lake during the late 1940's (Sabine National Wildlife Refuge Narrative Reports, 1940–1974) and again in the 1970's (Sprunt unpublished aerial survey data, National Audubon Society, Tavernier, Florida, 1974). Increased siltation at the mouth of the Atchafalaya River since the 1920's (Hebert, Louisiana Water Resour. Res. Inst. Bull. GT-1, 1–88, 1967) may have improved feeding and nesting habitat in Atchafalaya Bay, for in 1976, 2090 skimmers nested on unvegetated spoil islands in this area, with another 1000 nesting on the nearby Shell Keys.

Kopman (Bird Lore 9:233–240, 305–306, 1907) counted 1500 and 11,000 breeding...
skimmers on the Isles Dernieres and Timbalier Islands, respectively, in 1907. I counted 1032 active nests and 3084 adult birds on the Isles Dernieres, and 4863 adults on East Timbalier Island on 26 June 1976. This might indicate a regional decrease but might also represent a population shift to 2 large (and previously unreported) colonies that I noted near Barataria Bay. However, no definite conclusion is possible because Kopman did not specify whether he searched the Barataria Bay areas—the Barataria colonies may have been active in 1907 also.

Early records of colonial bird nesting at the mouth of the Mississippi River (Kopman 1907; Oberholser, Louisiana Dept. Conserv. Bull. 28:1-834, 1938) fail to mention Black Skimmers; therefore, present abundance on spoil adjacent to Southwest Pass probably developed as spoil deposition in that area created nesting habitat.

Shell berms at the seaward edge of the Chandeleur Sound salt marsh have been used traditionally by Black Skimmers. Kopman (Bird Lore 10:229-231, 1908) found 450, 400, and 500 adults nesting on Martin Island, Mitchell Key, and Brush Island, respectively; I counted 119, 457, and 166 adults on these 3 islands in 1976. Buchanan (Audubon Field Notes 3:242, 1949) reported 400 adult skimmers on Isle au Pitre in 1949; there were 1283 on 1 July 1976. On North Island, Valentine (pers. comm., U.S. Fish and Wildlife Service, Lafayette, Louisiana. 1975) estimated 1000 adults in 1968; I counted 335 adults in 1976. Although historic data are available on extant colonies, I cannot suggest regional trends because population shifts have probably occurred among such proximate groups (Fig. 1). Also, earlier observers (in boats) may have missed some marsh colonies, which would have been very conspicuous from aircraft.

Barrier beaches of the Chandeleur island chain have historically provided nesting habitat for skimmers. According to Bent (Bird Lore 12:280-282, 1910), 600 adults nested on Grand Gosier Island in 1910; I counted 2088 on 1 July 1976. Oberholser (1938) reported several hundred nests on Stake, Curlew, and Breton islands in 1933; there were 2558 adults nesting in these areas in 1976. The Breton Island colony had 100 nests in 1966, 750 nests in 1967, 100 nests in 1972 (Delta-Breton National Wild-

**Fig. 1.** Distribution and relative sizes of Black Skimmer colonies in coastal Louisiana, Mississippi, and Alabama, 1976.
life Refuge Narrative Reports, 1949–1974), 421 nests in 1974 (Valentine, unpublished) and 1938 nesting adults during our 1 July 1976 inventory. These data indicate a general increase for the barrier chain. However, Battledore Island, a large colony site 20 km west of Breton Island that included 3200 adults in 1908 (Kopman 1908), subsided and became a submerged reef by the 1950’s; emigration from Battledore could have contributed to the increases on Curlew, Breton, and Grand Gosier islands.

Imhof (pers. comm.) reported about 600 breeding adult skimmers on Dauphin Island in June 1956, 550 in May 1958, and 300 in May 1971; there were about 500 on this island in June 1956. Despite increased recreational vehicle traffic on Dauphin Island beach (Traylor, M.S. thesis, Univ. Alabama, Tuscaloosa, 1971), and the subsequent combination of several nesting groups into a single colony, the nesting population as a whole has apparently remained stable.

Colony distribution and size on the north Gulf Coast suggest habitat preferences of breeding skimmers. All colonies located during the 1976 survey were immediately surrounded by shallow estuaries. This would be expected if most skimming was conducted in shallow water (Zusi, Publ. Nuttall Ornithol. Club No. 3, 1962) and if the feeding range of nesters was limited to the waters immediately surrounding the colony (Tomkins, Wilson Bull. 68:236–239, 1951).

I found the largest colonies on expansive barrier beaches backed by extensive areas of shallow water, or on spoil islands in coastal shoals. Large regional populations, but small individual colonies, were also found on shell berms at the edge of the vast Louisiana salt marsh. In contrast, nesting was not observed in areas of limited estuarine development (between Calcasieu Lake and Shell Keys), or in estuaries where a hard unvegetated substrate was unavailable (salt marsh on the periphery of Barataria Bay lacking unvegetated berms).

These data indicate that skimmer nesting habitat requirements, shallow water feeding areas near a hard, extensive, and unvegetated substrate above the tidal reach, were best met by barrier beaches backed by extensive estuaries. However, increasing human recreational demands may effectively reduce undisturbed beach nesting areas, a process already observed on New York and New Jersey beaches (R. M. Erwin, pers. comm.). Fortunately, Gulf Coast spoil areas receive limited recreational use but are acceptable to breeding skimmers and can provide a useful alternative when human activities significantly affect reproduction on barrier beaches. Periodic dredging and spoil deposition, ideally scheduled during winter and early spring when birds are not nesting, would maintain skimmer nesting habitat by keeping the spoil unvegetated and above the tidal reach. (See Buckley and Buckley, Guidelines for the Protection and Management of Colonially Nesting Waterbirds, National Park Service, 1976:41–42; also Parnell and Soots, Proc. Conference on Management of Dredge Islands in North Carolina Estuaries, Univ. of North Carolina Sea Grant Program Publ., UNC-SG-75-01, 1974:35–46.)

Field data for this study were collected during an inventory of all colonially nesting birds of the north Gulf Coast conducted by the Louisiana Cooperative Wildlife Research Unit with support from the Office of Biological Services, U.S. Fish and Wildlife Service. J. B. Ortego, R. M. Ruhe, and M. Musgrove supplied able field assistance. W. C. Weber first called my attention to a skimmer colony on Horn Island, Mississippi. I thank R. B. Hamilton and R. M. Erwin for reviewing the manuscript and for suggesting significant improvements.—JOHN W. PORTNOY, Louisiana Cooperative Wildlife Research Unit, School of Forestry and Wildlife Management, Louisiana State Univ., Baton Rouge 70803. (Present address: 120 Amherst Rd., Pelham, MA 01002.) Accepted 1 Aug. 1977.
Killdeer breeding densities.—The Killdeer (Charadrius vociferus) is abundant throughout much of North America. There is, however, only limited information on Killdeer breeding densities. The present study was conducted between 12 April and 5 August, 1970 on approximately 113 ha of the St. Paul Campus, University of Minnesota, and the adjacent Minnesota State Fairgrounds.

The study area included 3 different habitat types: (1) open fields of mowed native grasses and weeds or untended dirt and coal (24 ha); (2) badly crumbled and unused asphalt areas of the fairgrounds (32 ha); and (3) agricultural fields (57 ha). Prior to 23 May, 75% of the agricultural field area was bare cultivated fields and 25% had plants higher than 15 cm growing in rows. After 23 May, the percentage of the agricultural fields with crops 15 cm or taller increased steadily, and by mid-July, virtually all the agricultural area had crops.

Killdeer sneak away from their nests if a human walks slowly into an area. Therefore, I searched for nests by running from concealment into an area and watching for Killdeer started off their nests, and then by returning to concealment and watching Killdeer return to their nests. Between 20 April and 1 July I checked the entire study area for nests approximately once every 4 days. A bow-net nest trap and mist nets were used to capture adult Killdeer at their nests. Chicks were located by watching for their movements while I ran into an area or by scanning with binoculars. They were caught by hand before they could fly. Age of chicks was estimated by body size and the stage of rectrix development, relative to chicks of known age. Each bird captured was banded with a USFWS metal band and 1 or 2 colored plastic bands. During this study neither all the breeding Killdeer were banded nor were all the nests on the study area found. However, it is likely that most of the chicks hatched on the study area were caught because chick movements were easily detected.

Fourteen breeding pairs of Killdeer were observed. Both individuals of 8 pairs were banded, and 1 member in each of the other 6 pairs was banded. These 14 pairs initiated 26 nests and hatched 13 chicks, all of which were banded. An additional 17 chicks from unfound nests of unmarked pairs were banded.

The population of the study area was estimated by the Lincoln Index method (Davis, Manual for the Analysis of Rodent Populations, Edward Bros. Inc., Ann Arbor, 1956) to be 67 adult Killdeer, based on the total number of sightings of banded adults (48) and unbanded adults (99). Observations were made of the entire study area, every day between 11 June and 11 July 1970, in order to get a large sample. The last adult Killdeer was banded on 11 June, and pre-migratory flocking non-residents had not yet appeared by 11 July. (Post-breeding population estimates of 234, 241, and 170 adult Killdeer were made on 21 July, 29 July, and 5 August, respectively.)

To determine if the entire population was breeding, I based a second population estimate on the number of chicks captured from the known nests of the marked pairs and the number of chicks captured from unknown nests of unmarked pairs. The rationale for this method follows. The young from known nests were all captured within 100 m of their nests and the chicks of a brood remain together, with their parents, until after attaining flight capabilities. Therefore, other groups of chicks captured on the study area must have been separate broods from unknown nests on the study area. Because average brood size and the estimated age of the chicks at capture are similar for chicks from known nests and from unfound nests (1.9 chicks/brood, 10 days and 1.7 chicks/brood, 15 days respectively) it is reasonable to assume equal productivity by the marked
and unmarked pairs. Based on this assumption, a calculation of the breeding population can be made by equating the ratios of marked pairs (14) to their chicks (13) and unmarked pairs (unknown) to their chicks (17). This yields an estimate of 18 unmarked pairs, and a total breeding population of 32 pairs of Killdeer.

This second determination (64 individuals) is remarkably close to the first (67 individuals). This agreement suggests that most of the population of the study area was breeding, and suggests the marked pairs are representative of the entire population. Thus it is reasonable to assume the habitat distribution of the marked pairs was indicative of the entire breeding population. Estimating a breeding population of 33 pairs and knowing the habitat distribution of the 13 marked pairs which had first nests prior to 23 May, it is possible to calculate approximate first nest breeding densities of the entire breeding population for the different habitat types (Table 1).

The literature on Killdeer breeding densities is scattered and difficult to interpret. On 16 ha of grazed, rolling grassland, 2 and 3 pairs of Killdeer occurred during 2 successive years (Holliday, Aud. Field Notes 1:219, 1947; Holliday, Aud. Field Notes 2:243-244, 1948). One pair of Killdeer bred on 11 ha of uncultivated prairie grassland during each of 3 years (Fairfield, Aud. Field Notes 16:431, 1962; Fairfield, et al., Aud. Field Notes 17:503-504, 1963; Fairfield, Aud. Field Notes 18:564, 1964). Speirs and Orenstin (Can. Field-Nat. 81:175-183, 1965) found Killdeer in 7 of 10 areas censused in Ontario County, Canada. The average density was 6.7 adult birds per 40 ha (range, 6 to 16 adult birds per 40 ha); presumably they were breeding birds for the censuses were taken in June. In this study I found breeding densities 2 to 5 times those of Holliday (op. cit.), Fairfield (op. cit.), and Speirs and Orenstin (op. cit.).

No single census method guarantees accuracy. The application of several techniques to the same population and comparison of the results allows critical evaluation of the accuracy of the estimates and if the results agree, increased confidence in their validity. In this study the census techniques are not completely independent. However, they do confirm that most of the population was breeding, and provide confidence in the accuracy of the population estimate.

I wish to thank Richard E. Phillips for his help during the field work and Donald A. Jenni for his suggestions and helpful criticisms of the manuscript.—TERRENCE R. MACE, Dept. of Zoology, Univ. of Montana, Missoula, 59812. Accepted 28 June 1977.


Brown Pelican restocking efforts in Louisiana.—The last natural nesting of the Brown Pelican (Pelecanus occidentalis) in Louisiana occurred in 1961 (Williams and Martin, Quart. J. Florida Acad. Sci. 31:130-140, 1969). Soon thereafter, it became evi-
Table 1

Florida Pelicans Sent to Louisiana and Their Subsequent Reproductive Success

<table>
<thead>
<tr>
<th>Year</th>
<th>Collection Site (Fla)</th>
<th>No. of Nestlings Taken</th>
<th>Number Surviving</th>
<th>2 Weeks After Release</th>
<th>No. of Young Fledged in Louisiana</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1968</td>
<td>Hall Island</td>
<td>50</td>
<td>49</td>
<td>46</td>
<td>no nesting</td>
</tr>
<tr>
<td>1969</td>
<td>Hall Island</td>
<td>55</td>
<td>53</td>
<td>50</td>
<td>no nesting</td>
</tr>
<tr>
<td>1970</td>
<td>Hall Island</td>
<td>100</td>
<td>100</td>
<td>94</td>
<td>no nesting</td>
</tr>
<tr>
<td>1971</td>
<td>Hall Island</td>
<td>65</td>
<td>65</td>
<td>63</td>
<td>8</td>
</tr>
<tr>
<td>1972</td>
<td>Hall Island</td>
<td>100</td>
<td>100</td>
<td>86</td>
<td>14</td>
</tr>
<tr>
<td>1973</td>
<td>Port Orange</td>
<td>100</td>
<td>100</td>
<td>97</td>
<td>26</td>
</tr>
<tr>
<td>1974</td>
<td>Port Orange</td>
<td>102</td>
<td>100</td>
<td>100</td>
<td>104</td>
</tr>
<tr>
<td>1975</td>
<td>Port Orange</td>
<td>103</td>
<td>101</td>
<td>97</td>
<td>13</td>
</tr>
<tr>
<td>1976</td>
<td>Crane Island and</td>
<td>58</td>
<td>99</td>
<td>72</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td>Port Orange</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>778</td>
<td>767</td>
<td>705</td>
<td>221</td>
</tr>
</tbody>
</table>

dent that if the species were to survive in Louisiana, a broad-based, cooperative reestablishment effort was needed. In 1966, a meeting of interested persons and agencies was organized by the Louisiana Wildlife and Fisheries Commission and the National Audubon Society. This meeting led to the formulation of a restocking program to be undertaken by the Louisiana Wildlife and Fisheries Commission and the Florida Game and Fresh Water Fish Commission. Birds were to be taken from stable colonies in Florida and introduced at historic colony sites in Louisiana. Secondary objectives of this study were: (1) to monitor for any lingering evidence of the factors responsible for the original demise of the species in Louisiana during the late 1950's to early 1960's, and (2) to compare the pesticide residue levels of Florida pelicans with those transplanted to Louisiana, thus providing some insight into the relative health of both environments.

Beginning in 1968, nestling Brown Pelicans, 8 to 11 weeks old, were captured from nesting colonies on Florida's Atlantic Coast (Brevard and Volusia counties) and trucked to Louisiana for release. The number of pelicans sent each year, the collection site, and number which survived are given in Table 1. Pelicans were released at 2 sites in 1968 and 1969, Rockefeller Refuge and Grand Terre Island (Fig. 1). The birds released at the Rockefeller Refuge site apparently died and all subsequent releases were made at Grand Terre. Direct release with 2 daily feedings was found to be the most effective method for establishing the birds in Louisiana.

Reproduction in transplanted birds first occurred in 1971 when the initial transplants became 3 years old (Williams and Joanen, Wilson Bull. 86:279-280). A total of 221 Louisiana-produced young were fledged between 1971 and 1976 (Table 1).

A well publicized die-off of both White (Pelecanus erythrorhynchos) and Brown Pelicans began late in the winter of 1975 and continued into summer. An estimated 35 to 40% of the standing population of 400 to 450 Brown Pelicans was lost. Earlier newspaper reports listed the loss as much higher, some accounts as high as 80%. Tissue
Fig. 1. Brown Pelican capture sites and release location for Louisiana restocking.

analysis indicated the presence of endrin (Florida Game & Fresh Water Fish Commission, unpublished data) which was probably the causative agent. The source of the endrin has not been identified.

The 1975 die-off points up the value of and need for a continuing monitoring effort. Had there been no pelicans present, the endrin contamination might have gone unnoticed until its effects would have been much more apparent. In the case of endrin, as with DDT (Anderson et al., Can. Field-Nat. 83:91-112, 1969), pelicans appear to be a highly sensitive organism responding quickly to environmental contamination.—Stephen A. Nesbitt and Lovett E. Williams, Jr., Wildlife Research Laboratory, Florida Game and Fresh Water Fish Commission, 4005 S Main Street, Gainesville, FL 32601, and Larry McNease and Ted Joanen, Louisiana Wildlife and Fisheries Commission, Grand Chenier, LA 70643. Accepted 18 July 1977.


Notes on 2 species of birds previously unreported from Peru.—While studying birds during June 1974 in the Departamento de Arequipa, Perú, 3 of us (Tallman, Parker, and Lester) found 2 species previously unreported in the republic.

Fulica rufifrons.—On the west coast of South America, the Red-fronted Coot was previously known to range north only to Atacama, Chile (Johnson, The Birds of Chile, Platt Establecimientos Gráficos, Buenos Aires, 1955). On 5 June 1974, Tallman and Parker obtained a specimen 3 km southeast of Mejia (9 km southeast of Mollendo) and thus extended the known range of the species about 1200 km. The bird, a female (LSUMZ 77955; skull ossified, largest ovum 2 X 2 mm; moderately fat with light molt), was one of a pair found in Scirpus sedge in a freshwater coastal marsh.

Hughes confirmed local breeding on 28 November 1974 by finding a pair with 2 small chicks in a marsh 2 km southeast of Mollendo. During 1975, he found F. rufifrons in small numbers in the marshes between Mollendo and Mejia and saw an adult feeding a chick on 16 December, 4 km northwest of Mejia. Since 1974, the population of this coot appears to have increased and it is occurring in sympathy with the larger-sized F. americana (American Coot) and F. ardesiaca (Slate-colored Coot). Gill (Condor 66:
209–211, 1964) considers the Slate-colored Coot to be a color morph of the American Coot.

*Conirostrum tamarugensis.*—Johnson and Millie (in Johnson, Supplement to The Birds of Chile, Platt Establecimientos Gráficos, Buenos Aires, 1972) reported the typical habitat of the recently described Tamarugo Conebill as mesquite groves, or “*tamarugales,*” (*Prosopis tamarugo*) in lowland northern Chile, but they mentioned possible sightings at higher elevations. On 15 June 1974, Tallman, Parker, and Lester found *C. tamarugensis* in a zone of low (1.5–3.0 m) scattered trees (*Polylepis* sp.) and shrubs (*Gynoxys* sp.) between 3450 and 3850 m above sea level on the slopes of Cerro Picchupichu, approximately 50 km northeast of the city of Arequipa.

The cone-bills foraged in groups of 4 to 10 individuals, feeding mainly at the higher elevations where *Polylepis* is dominant. The 4 specimens obtained (LSUMZ 79121-124), 3 males and 1 female, all had ossified skulls, showed little to moderate fat, and were molting on the heads and necks. None was in breeding condition. Unlike Johnson and Millie, we found no difference in plumage between males and females. This similarity in plumage is expected because of the adults of both sexes of the closest relatives of *C. tamarugensis*, *C. cinereum* (Cinereous Conebill), *C. rufum* (Rufous-browed Conebill), and *C. ferrugineiventre* (White-browed Conebill) are indistinguishable. Hughes later observed *C. tamarugensis* in the same area on 13 July and 14 September 1974 and on 7 June 1975. On these occasions, the birds were more in evidence among *Gynoxys* (3400–3500 m) with only a few in *Polylepis* (up to 3900 m). This cone-bill is not known in Peru below 3400 m.

Behaviorally, *C. tamarugensis* closely resembles *C. cinereum*, especially in its foraging manner, gleaning leaf surfaces and twigs of trees and shrubs, and in its call, a “seep” and a quarrelsome “*chicherichetache.*” On Cerro Picchupichu, the ranges of the 2 cone-bills overlap from 3400 to 3650 m, but only *C. tamarugensis* inhabits the upper limit of *Polylepis* at 3700 to 3900 m. *C. tamarugensis* probably breeds at high elevations and descends to low elevations at certain times of the year. It may replace *C. cinereum* as a breeding species in the *Polylepis-Gynoxys* habitat on the arid Pacific slope of the Western Cordillera of the Andes from southern Peru to northern Chile. In the lowlands of northern Chile, where *C. cinereum* breeds, *C. tamarugensis* may be a visitant.—Dan A. Tallman, Theodore A. Parker, III, Gary D. Lester, Louisiana State Univ. Museum of Zoology, Baton Rouge, 70893, and R. A. Hughes, Casilla 62, Mollendo, Peru. Accepted 5 July 1977.


**Responses of birds to a snowstorm in the Andes of southern Peru.**—Although there are a number of birds that regularly migrate north from Chile and Argentina to spend the nonbreeding season in Peru, relatively little is known about the elevational movements of these and other high-Andean species. Most birds that inhabit the high puna grasslands and *Polylepis* woodlands above timberline in southern Peru are thought to be resident and sedentary, but we have made observations demonstrating that some of them apparently do occasionally perform short-term elevational migrations in response to extreme climatic conditions and that behavior of both the resident and “migrant” species changes correspondingly when this movement occurs. These movements are comparable to those of certain alpine species of mid-latitude mountains such as the western North American rosy finches of the genus *Leucosticte*. The latter apparently undertake such downslope migrations only as part of their annual cycle, but during the
autumn months (Sept.–Nov.) they may move up and down the slopes depending on the amount of snow that falls at higher elevations (Bent and collaborators, U.S. Natl. Mus. Bull. 237 (1):382–383. 1968). Zimmer (Auk 55:405–410, 1938) reports altitudinal migrations for Cinclodes oustaleti in Chile, but Johnson and Goodall (The Birds of Chile and Adjacent Regions of Argentina, Bolivia, and Peru, Vol. 2, Platt Establecimientos Gráficos S.A., Buenos Aires, 1967) claim that the movement of this species also is performed only as an annual event and not in response to short-term extremes in climatic conditions.

From 7 to 11 August 1974 we were camped at the ruins of Peñas, on the western slope of the eastern Andes, about 25 road km above the Inca ruins and town of Ollantaitambo on the road to Quillabamba. Department of Cuzco, at an elevation of approximately 3262 m. The Peñas area is situated about 300 m below absolute timberline in a steep-sloped valley with a rushing mountain-sloped stream in its floor. The slopes are covered with bushes and small trees, some up to 6 m in height, and large boulders. In well-protected gullies and small canyons, alders (Alnus sp.) can be found.

On 8–9 August 1974 a massive cold front pushed northward into southern and central Peru. On the 9th, snow fell in the city of Cuzco for the first time in many years. At our camp rain fell most of the day, and by early evening it had changed to sleet, which continued until about 22:00. What we did not realize until the next morning was that the sleet had given way to falling snow. The temperature on 10 August remained near 0°C until about noon and snow continued to accumulate until that time, when approximately 15 cm was on the ground.

In the Peruvian Andes the temperature at 3262 m is rarely low enough to permit the formation of snow and even less frequently is it low enough to permit accumulation. At this low elevation the effect of the snow on the birdlife was evident in both the major influx of species and individuals from above timberline and the “confused” behavior of these and some resident species. Insectivorous, nectarivorous, and seedeating species were affected.

The first evidence of the influx occurred as we stood by our tent early in the morning. We noticed individuals of the insectivorous furnariid, Cinclodes fuscus, flying down the valley past us. After seeing about 6 in 3 min, O’Neill began to count them. In a period of approximately 15 min he counted 27 birds. We then became distracted by many other events and so throughout the rest of the morning only occasionally took note of the movement of that species. However, whenever either one of us looked up the valley he could see a Cinclodes making its way down out of the heavy snowfall that was occurring above.

We had specimens to prepare from the previous day and so were forced to spend time inside the tent. On each occasion that one of us went out, something new was encountered. Another furnariid, Asthenes uyattii, a grassland species, was atop a snow-covered bush. Parker walked along the highway, which was warm enough to remain relatively free of snow, and observed great numbers of displaced puna birds. Scattered aggregations foraged over the slush-covered gravel. These groups consisted of Asthenes humilis, A. flammulata virgata (not previously reported from the Department of Cuzco), and the finches Phrygilus unicolor, P. plebejus, and P. gayi. Before the snowfall only the last-mentioned of these had been present in the area, and from our experiences in other areas in Peru we would not have expected the other species to occur there under normal conditions.

Despite the weather conditions hummingbirds seemed to be as active as usual, but some had difficulty finding snow-free flowers (primarily Salvia spp. and Passiflora
spp.) and intra- and inter-specific aggression appeared to be more frequent than they had been before the snowfall, despite the added energy expenditures of such behavior. As soon as an *Aglaeactis castelnaudii* (wt. ca. 7 g), the most common resident species, attempted to feed at a flower that was not covered with snow, it was usually attacked by another individual of the same species or by an *A. cupripennis* (wt. ca. 7 g). The interactions between the two species of *Aglaeactis* occurred to such an extent that almost every time we began to watch an individual of either species, another bird would be after it. *Pterophanes cyanopterus* (wt. ca. 11 g) and *Metallura tyrianthina* (wt. ca. 3 g) were both active and were both regularly supplanted by the *Aglaeactis* species. Individuals of both *A. castelnaudii* and *M. tyrianthina* were sometimes hit by large, wet snowflakes and once the entire pile of snow covering a hanging flower fell on an *Aglaeactis* as it fed. The latter bird perched, shook, and preened, and then went on its way. Below the camp Parker collected a specimen of *Chalcostigma stanleyi* (wt. ca. 7 g), a species that we had previously encountered only in *Polyplepis* woodlands above the main timberline.

In the afternoon, after the snow ceased to fall and the sky began to clear, Parker went to a small plowed field close to camp. The field contained many members of the tyrantid genus *Muscisaxicola*. He collected 4 birds representing 4 species: *M. alpina grisea*, *M. cinerea*, *M. ruthifertix*, and *M. albiflora*, none of which had been present the previous day. None of the *Muscisaxicola* had enlarged gonads.

Resident birds noted that day included *Athenes ottonis*, *Cranialdeuca albicapilla*, *Myiotheretes erythropygius*, *Xenodaenys parina*, *Conirostrum cinereum*, *Diglossa carbonaria*, *Saltator aurantirosus*, and *Zonotrichia capensis*. These birds seemed to be foraging normally, but more than the usual number of *Zonotrichia capensis* were seen searching for food along the slush-covered gravel road.

No Gray-breasted Seedsnipes (*Thinocorus orbignyanus*) were noted, but 4 days later, after another big snowfall, O'Neill went over the pass above Peñas and flushed many flocks of them from the gravel roadbed. Since seedsnipes are probably not dependent upon insects, they are not likely to be greatly affected unless the snow stays on the ground for a long period of time. Even if the snow had remained, the seedsnipes, unlike the displaced finches and insectivorous furnariids and tyrannids, would probably have been able to uncover their needed food.

The night of 10 August was clear and a hard freeze ensued. The majority of the snow, however, had melted during the previous afternoon, when the temperature rose above 0°C. The morning of 11 August, cloud cover was high and all snow was gone. We were scheduled to leave the area, were busy breaking camp, and thus did not pay as much attention to the birds as we should have. We did, however, notice several *Cinclodes fuscus* flying up the valley, but not in the numbers in which we had seen them come down. On the same morning another puna-inhabiting finch, *Diuca speculifera*, was collected in the pasture below camp.

On 15 August O'Neill had the opportunity to talk to local people who lived on the other side of the pass from Peñas, and they informed him that the birds of the puna also come down to their area when there is a snowstorm. The sight of puna birds in the lush temperate forest of the eastern slopes is difficult to imagine!

Our observations show that, given the opportunity, some puna-inhabiting birds will move to lower elevations to escape heavy accumulations of snow. We wonder, however, what individuals of some of these same species do in parts of the vast south-Peruvian or north-Bolivian altiplano where there are no nearby lowlands to which to descend.

We wish to thank John S. McIlhenny of Baton Rouge for his continuing interest in
and support of the Peruvian fieldwork of the Louisiana State University Museum of Zoology, the institution that sponsored our studies. We also express our gratitude to Marc Dourojeanni R., Carlos Ponce P., and Antonio Brack E. of the Dirección General Forestal y de Fauna, Ministerio de Agricultura, and Hernandez de Macedo R. of the Museo de Historia Natural "Javier Prado," all of Lima.—John P. O'NEILL and Theodore A. PARKER, III, Museum of Zoology, Louisiana State Univ., Baton Rouge 70893. Accepted 28 July 1977.


Cannibalism by an Adult Great Horned Owl.—Reports of cannibalism in birds of prey are not uncommon, although in most cases the cannibalism has involved nestlings and has been deduced from post facto circumstantial evidence. Pilz (Auk 93:838, 1976), Heintzelman (Auk 83:307, 1966), and Ingram (Auk 76:218, 1959) have all documented cannibalism directed towards juvenile raptor birds. Cannibalism among birds of prey, however, has seldom been reported in the literature. Clevenger and Roest (Auk 91:639, 1974) observed possible cannibalism when they reported seeing an adult Red-tailed Hawk (Buteo jamaicensis) carrying the partially eaten remains of another hawk of the same species. Robinson (Wilson Bull. 66:72, 1954) saw a Burrowing Owl (Athene cunicularia) feeding on another Burrowing Owl, while Steffen (Auk 94:593, 1977) found skeletal remains and rectrices from an adult Red-tailed Hawk in a nest with a live immature chick.

The observation described below took place within a fenced test reactor area on the Idaho National Engineering Laboratory Site. This area is characterized as a cool desert shrub biome and is situated along the western edge of the upper Snake River Plain in southeastern Idaho. At 09:00 on 3 December 1974, we saw a Great Horned Owl (Bubo virginianus) feeding on another Great Horned Owl on snow covered ground. The feeding owl showed little alarm on our approach to within 3 m and continued to remove breast feathers. It then fed on exposed pectoral muscle tissue. Since the dead owl was limp and not frozen despite a minimum temperature of −12°C the previous night, we concluded that the owl had died recently.

On 2 subsequent visits within a span of 3 hours, the owl was still seen feeding on the carcass, however no further observations were made that day. The following morning at 08:30, a Great Horned Owl was again feeding on the remains, but flew when approached. The owl returned within a few minutes and continued to feed until 13:00 when it left; it was not seen again. Most of the flesh had been removed from the owl carcass and the head was severed from the body. The remaining skeletal mass and gastrointestinal tract were intact. Two castings were collected and one contained owl remains. A comparison of the remains, including the feet, with Great Horned Owl study skins at Idaho State University suggested that the dead owl was a male. Although the sequence of observed events led us to hypothesize the actual killing of an adult owl by another, no causal evidence was found to directly support such a contention.

This note is a contribution from the INEL Ecological Studies Program supported by the Division of Biomedical and Environmental Research, Department of Energy.—J. B. MILLARD, Dept. of Radiology and Radiation Biology, Colorado State Univ., Fort Collins 80523; T. H. CRAIG, Biology Dept., Idaho State Univ., Pocatello 83209; O. D. MARKHAM, Environmental Sciences Branch, Dept. of Energy, Idaho Falls, Idaho 83401. Accepted 1 July 1977.
Caching behavior of Screech Owls in Indiana.—Caching of prey items in nests with young by Screech Owls (\textit{Otus asio}) has been observed frequently (e.g. Van Camp and Henry, North Am. Fauna 71:9–13. 1975). Frazar found 16 horned pouts (\textit{Pisces: Ictalurus nebulosus}) in a nest cavity in Massachusetts in January (\textit{Bull. Nuttall Ornithol. Club} 3:80, 1877).

At 17:00 on 4 March 1975, 50 day-old chickens (\textit{Gallus domesticus}) were placed in an enclosure (3.6 $\times$ 2.1 $\times$ 2.4 m) in a barn near Centerville, Wayne County, Indiana. At 23:00 many chicks were missing, and a gray phase Screech Owl was flying about the enclosure. The owl was captured and held overnight for release away from the capture site. The owl’s crop was about \( \frac{1}{2} \) full.

Twenty-two dead chicks, 7 decapitated, were found on a shelf near the ceiling of the enclosure. Except for the 7 that were decapitated, none of the dead chicks showed any external damage. Two weeks later, 2 more chicks, obviously long dead, were found cached on the rafters above the enclosure. Thus, a total of 24 1-day-old chicks were apparently killed and cached in the 6 h period.

Screech Owls in northern Ohio do not have young in the nest before April (Van Camp and Henry, op. cit.), and observations for central Indiana indicate the same (J. B. Cope, unpubl. data). This second report of caching outside the nesting season adds further evidence that Screech Owls are extremely opportunistic.—JAMES B. COPE AND JOHN C. BARBER, \textit{Joseph Moore Museum, Earlham College, Richmond, IN 47374.} (Present address, JCB: \textit{Division of Birds, Room E-607, N.H.B., Smithsonian Institute, Washington, D.C. 20560.}) Accepted 29 Apr. 1977.

Attacks on Red-headed Woodpeckers by flycatchers.—During field studies in 1966, 1967, and 1970 at Robert Allerton-Park near Monticello, Piatt Co., Illinois, Alexa Noble (pers. comm.) and I saw Eastern Kingbirds (\textit{Tyrannus tyrannus}) (EK) and Eastern Wood Pewees (\textit{Contopus virens}) attack Red-headed Woodpeckers (\textit{Melanerpes erythrocephalus}) (RH) many times. I report our observations because the encounters were numerous, involved similar attacks by 2 species, occurred at the same time and locality in 3 different years, and involved taxonomically and morphologically distinct species.

On 22 July 1966 I saw 8-10 adult and juvenile Red-heads gathered along a 100 m border between a 45-year-old abandoned field and a younger field. They had nested in nearby woods. Adults were hawking flying insects, most of which they fed to the juveniles. Juveniles occasionally hawked also. As many as 6 birds were in flight simultaneously. Four kingbirds, presumably a family group, were hawking in the same vicinity. During about 75 min, 31 of 46 recorded encounters among the birds were kingbird attacks on Red-heads, usually as Red-heads performed sallies. Chases ceased when the woodpeckers landed. The 2 species often perched together with no apparent aggression. Other types of encounters were rare (RH on EK. 6; RH-RH. 5; EK-EK, 4). On 23 August 1966, an EK in similar habitat 600 m from the earlier site showed no aggression toward non-hawking juvenile Red-heads nearby. One RH supplanted an EK on a perch.

Only a few adult Red-heads were present along the same border on 7 July 1967. One EK attacked hawking Red-heads twice and a perching one once. Many more RH adults, but only 1 juvenile, were seen with at least 2 kingbirds on 22 July. Interactions were
not as intense or as frequent as in 1966; I saw only 3 attacks (EK-RH, 2; EK-EK, 1).

At the same place on 17 July 1970, Alexa Noble (pers. comm.) saw 7 juvenile and
2 adult Red-heads hawking. One conspecific perch supplant was seen. No kingbirds
were present, but an Eastern Wood Pewee entered the area and chased Red-heads on
10 hawking flights. Red-heads returned the attacks twice. At another site with 2 juvenile
woodpeckers, and EK attacked a hawking RH. Noble saw one attack by each of the
flycatchers on Red-heads at different nearby sites on 18 July.

Of 70 encounters, 70% were flycatcher-on-woodpecker attacks which occurred almost
always while woodpeckers were hawking, i.e. behaving like flycatchers. I believe the
flycatching behavior provoked the attacks. Other reports of aggression between pre-
sumed non-competitors have been interpreted similarly (e.g., Austin and Russell, Condor
cases involved tyrannids and were similar to ours in that attacks ensued only when
flight behavior resembling hawking occurred. However, the pursued species, a sparrow
and a wren, were not feeding nor were they potential feeding competitors. The woodpeckers
we saw were presumably hawking the same prey as the flycatchers were. Be-
cause the tyrannids mainly attacked hawking woodpeckers and ignored ones perched
nearby, I reject the idea that the actions were protective attacks on an image of a po-
tential predator by notoriously aggressive birds.

The attacks may have been responses to fortuitous or inappropriate releasers (Selander
court, Brace and World, N.Y., 1966) which could waste time and energy and lower
the fitness of the aggressor. Such behavior may persist because of negligible selective
pressure (Austin and Russell 1972) or because of genetic swamping from allopatric areas
(Selander and Giller 1953; Orians and Willson, Ecology 45:736-745, 1964; Mur-
ray, Ecology 52:414-423, 1971). On the other hand, the aggression may persist be-
cause it is advantageous. An individual which repelled images similar to its own could
be favored if the apparent similarities manifested a significant use of critical resources
such as habitat or food by the intruder (Miller, J. Anim. Ecol. 37:43-61, 1968; Reller,
Am. Midl. Nat. 88:270-290). Only a more detailed study could differentiate among the
possibilities.

Some information suggests the possibility for critical overlap between the flycatchers
and Red-heads. They all overlap in range and habitat in forest-edges, groves, and open
forests (Bent, U.S. Natl. Mus. Bull. 174, 1939; ibid. 179, 1942; Hesperheide, Auk 88:61-
74, 1971; Jackson, Condor 78:67-76, 1976; pers. obs.). Pewees and Red-heads may share

I made the observations while doing graduate research funded by the Department of
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of Entomology and Applied Ecology, Univ. of Delaware, Newark, 19711. Accepted 18
July 1977.


An analysis of Gila Woodpecker vocalizations.—Gila Woodpeckers (Melanerpes
utropygialis) are conspicuous for their vocal behavior (Bent, U.S. Natl. Mus. Bull. 174,
1939). Bendire (U.S. Natl. Mus. Spec. Bull. 3, 1895) and Gilman (Condor 17:115–136, 1915) listed 2 types of calls for them: one was described as the species’ “sociable” call and the second as a shrill “belly-aching” call.

The purpose of this study is to further describe Gila Woodpecker vocalizations and to analyze them spectrographically. Their location call (Call 1) is then statistically examined to determine which components are most variable among birds and therefore likely candidates for use in individual recognition. These results are compared to what is known for other groups of birds. Preliminary descriptions of Gila Woodpecker vocalizations and detailed information about the behavioral contexts in which they occur are presented elsewhere (Brenowitz, Auk 95:49–58, 1978).

I studied 9 pairs of Gila Woodpeckers at Red Rock, in Grant Co., New Mexico from 17 March 1973 to 20 March 1974. The study area consisted of several cottonwood (Populus deltoides) groves along the banks of the Gila River. This riparian zone extends less than 200 m from the river and borders on a narrow strip of irrigated farm land. Desert forms the remainder of the local habitat. Observation time was in excess of 400 h.

Vocalizations were recorded on a Uber 4000 Report-L tape recorder at a tape speed of 19 cm per sec with use of a Uber M514 microphone and, sometimes, a 61 cm diameter parabolic reflector. Analyses of vocalizations were carried out on a Kay Electric Company Sonagraph model 6061B with a model 6076C amplitude display and scale magnifier unit. Temporal components of calls were examined on sound spectrographs (frequency vs. time plots) produced with a wide band-pass filter setting and frequency components on spectrographs made with a narrow band-pass filter setting. Time and frequency measurements were made by placing transparencies marked with time and frequency scales over sound spectrographs. Three, randomly chosen sequences of Call 1 for each of 5 male birds were then compared in one-way analyses of variance. The specific components examined were: duration of the first note in the sequence, duration of the interval between the first and second notes in the sequence, and minimum and maximum frequencies of the first note in the sequence.

Call 1 presumably corresponds to the species’ “sociable” call. It is composed of uniform vibrato notes with a simple temporal structure but a rich harmonic structure (Fig. 1a). It has been likened to a call given by Flickers (Colaptes auratus) and resembles both the “pulsed ‘location’” call of Golden-fronted Woodpeckers (Melanerpes aurifrons) (Selander and Giller, Wilson Bull. 71:107–124, 1959) and the “Cha-aa-ah” call of Red-bellied Woodpeckers (Melanerpes carolinus) (Killham, Wilson Bull. 73:237–254, 1961). Call 1 also shares structural and functional characteristics with the “Churr” call of Red-headed Woodpeckers (Melanerpes erythrocephalus) (Bock et al. Wilson Bull. 83: 237–248, 1971). Pairs moving independently about their territories locate each other with this call. This call also is the Gila Woodpecker’s primary territorial display, and boundary disputes were often limited to prolonged exchanges of it from the location in dispute. Males gave this call more than did females (N = 438 for males, N = 78 for females).

The number of notes in a sequence was highly variable (\( \bar{x} = 4.8, \ SD = 4.8, N = 48 \)). The duration of notes ranged from 0.18–0.38 sec (\( \bar{x} = 0.24, \ SD = 0.04, N = 29 \)) and the interval between notes varied from 0.18–0.95 sec (\( \bar{x} = 0.46, \ SD = 0.18, N = 27 \)). The minimum and maximum frequencies of notes ranged from 0.6–1.3 kHz (\( \bar{x} = 0.9, \ SD = 0.2, N = 29 \)) and 1.1–2.3 kHz (\( \bar{x} = 1.6, \ SD = 0.3, N = 29 \), respectively. The length of notes differed significantly among birds (p < 0.002) while the interval be-
Fig. 1. Sound spectrographs of Gila Woodpecker vocalizations. la, Call 1; lb, Call 2; lc, Gravel Call; ld, Combination Call.
tween notes did not (p < 0.50). The minimum frequency of notes differed significantly among birds (p < 0.05) but the maximum frequency did not (p < 0.10).

Call 2 is a series of sharp, "pip, pip" notes with a complex harmonic structure (Fig. 1b). It is most frequently given in response to disturbance by humans and following vocalizations of other species such as flickers and Starlings (Sturnus vulgaris). Females gave this call more than did males (N = 48 for males, N = 109 for females) and it appears to serve as a general alarm call. Call 2 is sometimes used in conjunction with visual displays in agonistic encounters.

The number of notes in a sequence varied considerably (x̄ = 6.8, SD = 5.9, N = 46). The duration of notes ranged from 0.08-0.14 see (x̄ = 0.10, SD = 0.01, N = 29) and the interval between notes varied from 0.10-0.34 see (x̄ = 0.21, SD = 0.14, N = 29). The minimum and maximum frequencies of notes ranged from 0.8-1.5 kHz (x̄ = 1.2, SD = 0.2, N = 29) and 1.3-1.6 kHz (x̄ = 1.4, SD = 0.1, N = 29), respectively. Call 2 was not examined for individual differences.

Gravel Call is composed of harsh rasping notes which are spectrographically similar to the notes of Call 1 although of shorter duration and with emphasis of different harmonics (Fig. 1c). The latter may explain its harsh sound. Gravel Calls were heard infrequently and only in situations in which Gila Woodpeckers appeared to be greatly agitated. One such instance involved the arrival of several Starlings in the nest cavity tree of a pair with young. This call was recorded too infrequently to permit a detailed analysis of it.

Combination Call consists of a first note similar to the notes of Call 1, followed by several notes similar to the notes of Call 2 (Fig. 1d). This may be an example of "ambivalent behavior" (Hinde, Animal behavior. A synthesis of ethology and comparative psychology, McGraw-Hill, New York, 1970), which is a single behavior containing components of conflicting tendencies (e.g., self-advertisement and alarm). I heard it only twice, both times while a male was being harassed by humans.

While some woodpeckers give as many as 13 different vocalizations (Ligon, Auk 87: 255-278, 1970), Gila Woodpeckers regularly use only 2. The 2 other calls in their repertoire, which are given only infrequently (Gravel Call and Combination Call), are either permutations or combinations of these calls. Despite these facts, vocalizations appear to be the Gila Woodpecker's most important form of communication. These calls could encode considerable information by variation in the number of notes in a sequence and also by variation in the intensity (sound pressure level) of notes. The behavioral context in which calling occurs (e.g., accompanying visual displays) can be altered as well.

In discussing individual recognition in passerines, Falls (Proc. 13th Int. Ornithol. Congr., pp. 259-271, 1963) indicated that there may be greater variance in frequency components than in temporal components of songs. Of the latter, the duration of notes may contain more variance than the interval between notes. Recently, Brooks and Falls (Can. J. Zool. 53:1749-1761, 1975) experimentally demonstrated that in White-throated Sparrows (Zonotrichia albicollis) individual recognition is based on frequency rather than temporal components of songs. There is evidence that the general rules concerning variance of passerine song components apply to Burrowing Owls' (Athene cunicularia) primary song, as well (Martin, Auk 90:564-578, 1973).

The most variable components of the Gila Woodpecker's location call (Call 1) are the duration of notes and the minimum frequency of notes, in that order. Information about an individual's identity may be contained in either the overall frequency sweep of its vibrato notes or in the minimum frequency itself. Based on the results presented
here it appears that a temporal component (the length of notes) may be important in individual recognition in this picine species. In this respect, Gila Woodpeckers appear to resemble larids and alcids (Beer, Adv. Study Behav. 3:27-74, 1970). These findings suggest that they may use an alternate means of individual recognition than is found in passerines and owls.

I am grateful to J. D. Ligon for his help with this study. I would also like to thank S. Alexander who was invaluable in helping to analyze sound spectrographs and J. A. King who read an earlier draft of this manuscript. This research was supported by grants from the Josselyn Van Tyne Fund of the American Ornithologists’ Union and the Student Research Allocation Committee of the Graduate Student Association of the University of New Mexico.—Gene L. Brenowitz, Dept. Anatomy, The Medical College of Pennsylvania, 3300 Henry Ave., Philadelphia, 19035. Accepted 11 Jan. 1977.


An aggressive encounter between a Pintail with a brood and a Franklin Gull. —Gulls are known to prey upon waterfowl nests (Odin, Auk 74:185-202, 1957). Recent studies, however, have shown that insular nesting ducks have high hatching success but low fledging rates when nesting in association with larids (Vermeer, Wilson Bull. 80:78-83, 1958; Dwernychuk and Boag, Can. J. Zool. 50:559-563, 1972). Dwernychuk and Boag (op. cit.) suggested that gulls provide protection for nesting ducks by mobbing potential avian egg predators, but that adult gulls kill newly hatched ducklings when their young are able to consume prey of such size. Most predation occurs while young ducklings are on open water.

On 21 June 1976 we observed an aggressive encounter between a female Pintail (Anas acuta) with a brood and a Franklin Gull (Larus pipixcan) near Boissevain, Manitoba. The brood of 5 downy young swam from emergent cover onto a pond of about 15 ha. Other dabbling ducks were present as were about 200 Franklin Gulls. Our attention was diverted from the brood momentarily, and although we did not see a gull attack the brood, a fight ensued. The Pintail hen held the gull in her bill, beat it with her wings, and kept it partially submerged for about 5 min. Meanwhile, the brood swam to a group of adult ducks and remained there in a tight group. No gulls attacked the brood in the absence of the hen. The Pintail returned to her young at the end of the fight and they re-entered emergent cover. The Franklin Gull, although not dead, had difficulty swimming and appeared to have suffered a broken wing. We suggest that some individual ducks do recognize gulls as being dangerous and give this observation as evidence of brood defense.—George Hochbaum and Garth Ball, Canadian Wildlife Service, 501 University Crescent, Winnipeg, Manitoba. Accepted 30 Mar. 1977.


Canada Goose-Great Blue Heron-Great Horned Owl nesting associations.—While conducting nesting studies of Great Basin Canada Geese (Branta canadensis moffitii) along Rufus Woods Reservoir on the Columbia River in Okanogan and Douglas counties, Washington, we witnessed an interesting series of successful displacements of nesting Great Blue Herons (Ardea herodias) by Canada Geese. This appears to be the first such account of nesting displacements between geese and herons, although Craighead and Stockstad (J. Wildl. Manage. 25:363-372, 1961) observed different amounts of tree nesting by Canada Geese between years and felt this difference was due to a
differing ability of Ospreys (*Pandion haliaetus*), eagles, herons, and Red-tailed Hawks (*Buteo jamaicensis*) to deter geese from using these sites.

A ponderosa pine (*Pinus ponderosa*) situated along the reservoir shoreline which contained 10 inactive Great Blue Heron nests experienced the following nesting regime. Nesting was initiated on 20 March 1975 by a pair of Great Horned Owls (*Bubo virginianus*) which nested in the top-most heron nest approximately 30 m above the ground. Within 2 days a pair of Canada Geese began nesting in an adjacent heron nest. On 28 March 2 pairs of Great Blue Herons occupied 2 more existing nests and at least one egg was laid. On 29 March these 2 Great Blue Heron nests were occupied by 2 additional pairs of geese. These geese displaced the heron egg(s) and laid eggs of their own. These nests were eventually deserted. The owls also deserted after incubating 4 infertile eggs for over 50 days. The first pair of geese successfully hatched a clutch of 5 eggs. The owl, goose, and heron nests occurring in this tree were within 9 m of each other. On several occasions the geese and owls were observed on their respective nests with no inter- or intraspecific strife observed.

On 30 March 2 pairs of Great Blue Herons constructed 2 nests in adjacent pines 5 km downstream from the above mentioned tree. The following day both heron nests had been usurped by Canada Geese. One pair of geese eventually hatched a clutch of 4 eggs; the other pair deserted. The latter nest was an extremely flimsy structure in a dead tree. The displacements of herons by geese occurred during a 1-2 day period although no interspecific interactions were actually observed. The herons subsequently left the area and no herons were seen again on the reservoir until several weeks later.

D. A. Manuwal, W. H. Oliver, D. R. Paulson and J. B. Atchearn were kind enough to read drafts of this paper and offer helpful criticisms.—Richard L. Knight, Washington Dept. of Game, 509 Fairview N., Seattle 98109; and Albert W. Erickson, Wildlife Science Group, College of Fisheries, Univ. of Washington, Seattle 98195. Accepted 12 May 1977.


**Giant Canada goose incubates eggless nest.**—On 9 May 1970, M. S. Phillips and I found a Giant Canada Goose (*Branta canadensis maxima*) incubating at a nest with no eggs in it. The nest was located on a small island on Seney National Wildlife Refuge in Michigan’s Upper Peninsula. The goose allowed us to approach to within 5 to 6 m of the nest before flushing. Prior to flushing, she maintained the typical flattened, stretched out posture. The nest was well constructed, lined with a large amount of down, and typical of one that would normally contain 5 or 6 eggs. There was no sign of predation or anything else that might have resulted in the loss of the clutch. The goose quickly returned to the island and resumed her position on the nest upon our departure.

This bird was particularly interesting because she had been color-marked as an adult female on 3 July 1953. Thus, she was at least 8 years old when found on the eggless nest.

Because of the neck collar, she was earlier identified with a mate (sex unverified) on and around her nesting island. She remained on the nest for another week following my visit. About the peak of the refuge goose hatch, 16 May, she left her nest and was not seen again until 4 September, when she reappeared near the nesting island.

Refuge records since 1953 do not mention this bird being seen with a brood, although she was recorded on the refuge at least in 1967 and 1969. When captured in 1963, she was with a group of non-breeders. Further, nest records revealed that she had never...
previously been observed on a nest, even though complete nest searches of the refuge have been made annually since 1963. Apparently, this bird was not a productive member of the flock, although something stimulated her to go through all the motions in 1970. She was not seen again after the 1970 nesting season.

Similar behavior was recently reported for a Wood Duck (Aix sponsa) in Massachusetts (Heusmann and Pekkala, Wilson Bull. 83:148-149, 1976). In this case, the hen tended an eggless nest for 3 successive breeding seasons. In the third year, she was provided with a clutch that was successfully incubated and hatched. Later evidence indicated at least partial brood survival.

While these 2 cases may represent nothing more than aberrant behavior, they do raise questions about the breeding cycle of birds. Parasitic nesting demonstrates the ability of some species to biologically complete the breeding cycle even though it is not behaviorally completed. These 2 waterfowl cases suggest that there may be secondary stimuli that can produce a behavioral completion of the breeding cycle even though a biological completion is not possible.—CONRAD A. FJETLAND, U.S. Fish & Wildlife Service, P.O. Box 250, Pierre, SD 57501. Accepted 28 July 1977.


Nesting success and nest site selection of Red-winged Blackbirds in a freshwater swamp.—The ability of the Red-winged Blackbird (Agelaius phoeniceus) to nest in diverse habitats and different species of vegetation has been noted by Campbell (Wilson Bull. 60:244, 1948), Beer and Tibbitts (Flicker 22:61-77, 1950), Case and Hewitt (Living Bird 2:7-20, 1963), Meanley and Webb (Chesapeake Sci. 4:90-100, 1963), and Stowers et al. (Wilson Bull. 80:320-324, 1968). The selection of nest sites by Red-wings is presumed to be an indication of a site’s greater potential for nesting success. Our study was conducted to determine if Red-winged Blackbirds in a freshwater swamp exhibited any preference for nesting substrate and to determine if the location of the nest within the vegetation had any effect on the success of a nesting attempt.

From May to July 1975, an area receiving little human use was searched in Miller’s Lake, Evangeline Parish, Louisiana for Red-winged Blackbird nests. The study area consisted primarily of open, common buttonbush (Cephalanthus occidentalis) and Carolina ash (Fraxinus caroliniana) swamps.

The 136 nests found were each marked and subsequently examined for the presence of eggs and young. If a nest examined did not contain young, it was revisited at least once after a 1-week interval.

The supporting vegetation was noted and at 100 randomly selected nests, measurements were taken of the height of vegetation and the distances of the nest from the ground, water, and top of the supporting vegetation. A Student’s t-test was used to test if the distance of the nest from the water and from the top of the supporting vegetation differed between successful (young present) and unsuccessful nests.

The vegetation substrate of Red-winged Blackbird nests was determined for the 136 nests. Because nests were located no further than 2 m from the edge of any supporting vegetation, the amount of edge of each type of potential supporting vegetation was measured and the edge frequency composition was compared, using a Chi-square test, to the frequency composition of nest substrate species present.

Nesting sites.—Of the 100 randomly selected nests located in common buttonbush, 81 did not contain young. These nests averaged 1.26 m above the water and 0.49 m from the
top of the supporting vegetation. The 19 successful nests averaged 0.97 m above the water and 0.51 m below the top of the supporting vegetation. Successful nests were significantly lower than unsuccessful nests (t = 2.40, p < 0.05), but no differences were found in the distances from the top of the supporting vegetation (t = 0.28, P > 0.05).

These differences in success at different nesting heights are contrary to the findings of Meanley and Webb (1963) who studied the nesting of Red-winged Blackbirds in the tidal marshes of Maryland and found that nest success increased with height above ground or water: 45% for <0.6 m, 55% for 0.6–1.2 m, and 62% for >1.2 m. They attributed the reduced success rate of lower nests to easier accessibility by predators.

In our study, poor nest success is attributed to abandonment of nests after disturbance, avian predation, or weather damage. Higher nest success in the lower vegetation might be due to the relative lack of ground-dwelling mammalian and reptilian predators and to the increased stem density of the lower vegetation. The increased stem density could provide better concealment from avian predators and protection from weather.

Nesting preference.—In the study area, the relative abundance of potential nesting substrate species (expressed as amount of available edge) was common buttonbush, 11.2 km; southern wild rice (Zizaniopsis miliacea), 3.4 km; black willow (Salix nigra), 3.3 km; Carolina ash, 1.8 km; water elm (Planera aquatica), 0.4 km; water tupelo (Nyssa aquatica), 0.2 km; and red maple (Acer rubrum), 0.1 km. Nests were found in common buttonbush (131), southern wild rice (3), and black willow (2). A very highly significant (χ² = 131.51, P < 0.001) preference was found for Red-winged Blackbirds nesting in common buttonbush.

Common buttonbush was a more important Red-winged Blackbird nesting substrate species than southern wild rice because the basic woody nest-supporting structure of common buttonbush was present when the birds started nesting and southern wild rice was too short to support nests. Common buttonbush also had a shrubbier form, lower height, and provided more concealment to nests than other woody species present.

There were insufficient nesting attempts in other species of woody vegetation to determine if differences in nesting success existed between them and common buttonbush. We believe that the almost exclusive selection of common buttonbush as a nesting substrate indicates that it provides the best nesting conditions in this swamp habitat.—


Extreme nesting dates for the Mourning Dove in central Illinois.—The Mourning Dove (Zenaida macroura) is known for producing multiple broods over a prolonged nesting season. Nice (Auk 40:37–58, 1923) observed active nests in Oklahoma from late March into early October and cited reports of rare nesting from late January into December in Texas and California. In the central states, based upon a 3-year study in Iowa involving 3878 dove nestings, McClure (Trans. N. Am. Wildl. Conf. 15:335–346, 1950) calculated an average breeding season of 159 days from 4 April to 10 October. He further recorded extreme dates of 23 March to 15 October in Iowa and 8 April to 23 September in Nebraska. Bent (U.S. Natl. Mus. Bull. 162:416, 1932) listed “Indiana to Iowa” egg dates of 4 April to 1 September for this species. In a detailed analysis of 1950–58 dove nesting phenology in conifer plantings in northern and
central Illinois, Hanson and Kossack (Ill. Dep. Cons. Tech. Bull. 2, 1963) cited no specific nesting extremes but reported a breeding season from late March into September with only 1.6% of 1042 nests initiated after 4 August. The latest nesting activity of doves recorded for Illinois was a fledgling in Quincy on 10 November described by Angus as "so young that it was almost too small to leave the nest" (Bird-Lore 36:172, 1934). My data on 4 nests in the vicinity of Charleston in east-central Illinois indicate that nesting sometimes extends from middle March into early November.

On 20 October 1973 at the outskirts of Charleston (39°30'N, 88°10'W), I flushed an adult Mourning Dove from its nest containing 1 egg. The nest, 2.1 m high in a hawthorn (Crataegus sp.), was fully exposed due to nearly complete leaf fall. The adult was seen incubating on 3 later dates, but on 2 November it flushed with a broken wing display disclosing a small chick. The adult was noted brooding the next 4 days but on 8 November the first snowfall of the season deposited 1.9-2.5 cm by 17:00 followed by an overnight low of -5.6°C. At 07:00 on 9 November I found the adult absent and the young dove frozen in the nest, surrounded but not covered over by snow. Based upon aging criteria of Hanson and Kossack (1963), a body length of 43 mm and lack of primary quills on 2 November indicated an age of 1 day. This estimate combined with a 14-day incubation period established the probable laying date as 18 or 19 October. Measurements of the dead nestling were more typical of a 6 or 7-day-old squab suggesting some stunted development.

A second active dove nest approximately 47 m from the first was found on 30 October 1973 by Mrs. Wayne D. Coleman. This nest was 4 m high in a bare cherry (Prunus sp.) and contained 2 large squabs. On 1 November, 1 bird fledged soon after dawn and by noon the nest was empty. As I approached the nest site at 16:30, both fledglings flushed from the ground below and flew strongly some 10 m to elevated perches where I observed them to be well feathered except for short tails. I last saw the 2 near the site on 9 November.

A third late autumn nest was reported to me by Richard D. Andrews from his farm 9.6 km SE of Charleston. On 27 October 1973, he flushed an adult Mourning Dove from a nest in a honey locust (Gleditsia triacanthos) revealing 1 egg and 1 young dove covered with "big pin feathers." On 4 November this nest was empty except for numerous droppings.

Presumably initiated by increasing photoperiod or ameliorating climate, the breeding season for this multi-brooded species might well be extended by exceptionally mild autumn temperatures. At the Charleston weather station the 1973 mean monthly temperatures of 21.5°C in September and 16.6°C in October were 2.4 and 2.7°C above normal. The first official freeze occurred on 3 November compared to an average 16 October date. In Springfield, Illinois, the heating-degree-day total for July through October, 1973 was 35% warmer than the 30-year mean (U.S. Dep. Commerce, Climatological Data, 1973).

On 6 March 1974, a Mourning Dove carrying a stick into a grove of Austrian pines (Pinus nigra) on the Eastern Illinois University campus in Charleston provided my earliest nesting evidence for central Illinois. Actual nesting was not further observed but on 11 April 1975 in the same pine grove I discovered 2 dove fledglings I judged to be at least 2 days out of the nest. With a 14-day incubation plus 9-12 days to fledging (Hanson and Kossack 1963), these birds must have hatched from eggs laid before 18 March. These combined observations indicate a maximum nesting season of at least 230 days for this species in central Illinois.

I appreciate the advice and assistance of Richard D. Andrews and Dallas A. Price of Eastern Illinois University and Richard R. Graber of the Illinois Natural History Sur-
vey in the preparation of this manuscript.—L. BARRIE HUNT, Dept. of Zoology, Eastern Illinois Univ., Charleston 61920. Accepted 31 July 1977.


A volumetric analysis of Sharp-tailed Grouse sperm in relation to dancing ground size and organization.—Although the lek, or dancing ground display and mating behavior of *Pediocetes phasianellus* has been described by several authors (reviewed in Hjorth. Viltrey 7:184–596, 1970), histological and physiological correlates of lek behavior have received less attention (Trobec and Oring. Am. Midl. Nat. 87:531–536, 1972). Since most matings are known to occur near the center of the dancing ground (Hjorth op. cit.), the present study was designed to investigate the hypothesis that levels of testicular sperm are greater in males located centrally compared with males located at the periphery of dancing grounds. The additional possibility that levels of sperm are lower for males on smaller grounds (<10 males) was also examined.

Sixty-four males were collected from grounds of known size in central Manitoba. Whenever possible, 4 males were collected each week, 2 from a large and 2 from a small dancing ground, during 2 successive breeding seasons. For small grounds, a random sampling technique was used to determine which male was to be collected. For large grounds (10 or more males present), 1 male whose territory was near the center, and 1 from the periphery, were collected each week. Within 10 min of collection, a gonad was removed, the volume measured by water displacement in a graduated cylinder, and tissue samples fixed in Bouin's solution. Subsequent sections 7 μ thick were stained by Masson's trichome technique (Culling. Handbook of Histopathological Techniques, 1963, Butterworths, London). For quantitative assessment of sperm, the method of Chalkley (J. Cancer Inst. 4:47–53, 1943) was used. Structures lying under the tips of 4 pointers located in the eyepiece of a microscope were recorded as "hits." The procedure was repeated by moving the stage a short distance along a zigzag course through the section, for a total of 175 times per testis. The relative frequency of "hits" on any particular cell type, including sperm, was taken as the relative volume occupied by cells of that type. For statistical comparison between the different groups of males sampled, we used a sign test ($\chi^2$) based on comparisons between pairs of birds collected during the same week from different positions within large dancing grounds (central versus peripheral) or between large and small dancing grounds (small versus central, and small versus peripheral).

All birds collected during the breeding season appeared to be physiologically capable of breeding. No differences ($P > 0.05$) were present in overall testis volume among the three groups of males. Differences were, however, present in the relative volume of sperm present in the testes (Fig. 1). For both years combined, males located centrally on large dancing grounds possessed a significantly greater mean level of sperm than did the peripheral birds on the same grounds ($P < 0.001; \chi^2 = 16.0$). The volume of sperm for males from small grounds was also significantly greater than that of peripheral males from large grounds ($P < 0.01; \chi^2 = 9.0$). Differences between males from small grounds and central birds from large grounds, although present in both years (Fig. 1) were not significant ($P > 0.05; \chi^2 = 1.2$).

Although the relationships between central and peripheral birds from large dancing grounds and birds from small grounds tended to be similar for both years in which collections were made, levels of spermatozoa reached peak levels appreciably later in the
Fig. 1. Volume of spermatozoa in testes of central and peripheral males from large dancing grounds, and males from small grounds, at successive weekly intervals during the (A) 1967 and (B) 1968 breeding seasons. (Numbers in parentheses indicate total sample size.)
season in 1967 than in 1968 (compare Fig. 1, parts A and B). Peak attendance of
females at the lek was also later, by up to 3 weeks in 1967. The spring of 1967 was colder
and more extended than in 1968, as indicated by the mean monthly temperature for
April, which was 3.7°C lower in 1967. These results raise the possibility that spring
temperatures may act as modifiers to influence the gonadal cycle in this species (cf

The hypothesis that the testes of central males on large dancing grounds achieve
higher volumes of sperm than do those of males located at the periphery was supported
by the data. Whether there is a causal relationship between sperm volume, position
on the dancing ground, and proportion of total matings done by a particular male
awaits further study. Considered functionally, however, the results raise the definite
possibility that the central birds are best suited, biologically, to perform the majority of
matings on large grounds. The further possibility that males from large dancing
grounds have larger sperm volumes than those from smaller grounds was not supported,
in that males from small grounds had significantly larger sperm volumes than peripheral
males from large grounds, and did not differ significantly from central males on large
grounds. The latter result suggests that males on small dancing grounds should be no
less able to fertilize receptive females than are males from central locations on large
grounds. The possibility remains that differences in social stimulation may act in other
ways to reduce the reproductive success of small leks. Further studies are clearly re-
quired to assess this and other possible behavioral and histological correlates of dancing
ground size and organization.

This work was supported by grants to R. M. E. from the Manitoba Department of
Mines, Resources and Environmental Management, and an operating grant from the
National Research Council of Canada.—WAYNE M. NITCHUK AND ROGER M. EVANS,
Dept. of Zoology, Univ. of Manitoba, Winnipeg, Manitoba, R3T 2N2, Canada. Accepted
1 July 1977.
PRESIDENT'S PAGE

Everyone is well aware of the inflationary spiral that has occurred in recent years, and the costs of running an ornithological society has not escaped this process. The bulk of our expenditures relate to publishing The Wilson Bulletin; these rise with the ever increasing costs of ink, paper, and supplies. From 1976 to 1977 alone there was a 15% rise in printing costs. As a result the Society's income has steadily fallen behind annual expenditures. It became apparent from the Treasurer's report to the Executive Council at the past annual meeting in West Virginia that this financial deficit had become critical. Treasurer Ernest Hoover announced that costs had risen so much that we currently were paying for 2 back issues of the 1977 volume of the Bulletin out of 1978 dues income. Obviously this condition could not continue very long before there would be no funds for future issues.

An ad hoc committee chaired by James Karr considered the problem and rejected the possibility of using endowment funds to cover deficits because this measure eventually would lead to bankruptcy. Also it was decided not to recommend reducing the size of the Bulletin, which would only exaggerate the current pressures felt by ornithological journals and ornithologists, i.e., increasing numbers of papers submitted and through space limitations too many good ones rejected. It was concluded that the ornithological community simply would have to "bite the bullet" and adequately support The Wilson Bulletin. This required increasing both dues rates and publication page costs. These recommendations were adopted at the meeting.

New dues for individual members are $14.00 per year. Student members will continue to pay $10.00 a year, but may do so for only 4 years. They can apply to a life membership the total student dues paid if this option is initiated immediately on graduation or at the end of the 4-year period, whichever comes first. Institutional memberships are now $20.00, couples can join for $16.00, and life memberships become $250.00. (Membership dues were upped $2.00 in 1976, but this increase proved inadequate.)

The new page cost charge for papers published in The Wilson Bulletin is $55.00 per page. Recognizing that some authors cannot pay this, authors who are members of the Wilson Ornithological Society can apply to the editor for a grant from the Society covering up to $50.00 per page of the page cost. However, a grant is limited to a maximum of 12 pages per article, and a total of 20 such pages per author per year. Authors who are student members can apply for a grant covering full page charges.

The committee estimates that the increased income from the sources described above will eventually eliminate the spending deficit and will also keep pace with current expenditures. The Executive Council in the past has been handicapped in perceiving the overall financial condition of the Society by not having at hand a prospective budget for the upcoming year. The budget for 1977 was not sufficient by itself. Therefore, I asked Horace Jeter to compile a projected budget for use at the West Virginia meeting. This proved very useful and the practice will be continued.

A measure that will save the Society money in the future also was adopted by the Council. The Society will support together with the American Ornithologists' Union a central membership office charged with compiling and maintaining a computerized joint membership list for use in mailings for both organizations. The Cooper Ornithological Society has been asked to join the enterprise too and will decide later. Because of the many people that belong to all 3 or 2 of the 3 organizations, there has always been duplication in the 3 membership lists. Compiling a joint list will eliminate this duplication at a saving to the organizations. Even so, the system will recognize who belongs to which organization or organizations in mailing journals and so forth.—Douglas James.
FIFTY YEARS OF THE WILSON ORNITHOLOGICAL SOCIETY*

In 10 more years the Wilson Ornithological Society will celebrate its 100th birthday. Having reached the ripe old age of 4 score and 10, it seems fitting that we look backward in appreciation of the Society’s progress over the years.

A few of us—fewer than 20—have been members for 50 years or more. These have been privileged to share membership with Founders of the Society. Lynds Jones and R. M. Strong, both Founders, were still living in 1950. With this bridge we can span the entire 90 years of the organization’s existence.

Of course it was not organized as The Wilson Ornithological Society; the founders thought of it as a club for persons of like interests, and they named it The Wilson Ornithological Club. So it remained until the mid-50’s of the present century. At that time personal income taxes, and the exemptions which might be claimed for scientific travel, dictated the change of name. The I.R.S. was inclined to look more favorably on claims for attending a Society meeting than a Club get-together.

When a roll of members was published in 1902, it listed 60 active members. These included T. S. Roberts, of Minnesota; Norman A. Wood, of Michigan; V. E. Shelford, of Illinois; Francis Hobart Herrick, of Ohio; and others whose names have loomed large in the ornithology of mid-America. Lynds Jones, of Oberlin, Ohio, served the Club as its President during two widely-separated periods, and his tenure as Editor of The Wilson Bulletin spanned 34 years.

The patriarch of the modern Wilson Society, in point of membership, is Alexander Wetmore, who joined in 1903, the year the Wright Brothers took wing from Kill Devil Hill. No other living member has seen more than 65 years of the Society’s unfolding history. As stated previously, about 20 living persons have been affiliated for 50 years or more. A goodly number of these have been active in Society affairs, and so have had privileged views of its activities.

My own membership dates from 1927. Early in my tenure I began to attend annual meetings of the Club, and have been eternally grateful that I had these opportunities. I saw many of the persons whose names were appearing in The Wilson Bulletin; I met some of them, and they became personalities whom I would remember the next time.

At one of my early meetings Jesse M. Shaver, of Tennessee was President, and he was followed in office by Josselyn Van Tyne. What made this association remarkable was that both these men were 6 feet, 8 inches in height. Seeing them together on the platform was overwhelming. Such stature was extraordinary in those days; we had not then begun through some sort of Lamarckian genetics to produce human beanpoles to meet the demands of the National Basketball Association.

Jesse Shaver commented on the circumstance. He recounted that he had been in Pittsburgh a few years previously, and had noted people looking at him speculatively as he moved over the University of Pittsburgh campus. “Now,” he said, “I return to find the Cathedral of Learning here!”

A few years before the outbreak of World War II, I became the Club’s Secretary, through this connection I was privileged to have inside views of the Club’s traumas and struggles during the war years. Many of our finest young men and women were in service. Gasoline was severely rationed, and most automobile travel was out of the question. Travel by train was uncomfortable and exhausting; persons in uniform took priority; dining was sparse or non-existent; everything civilian gave way to the exigencies of war.

* Text of the banquet address given by past-president Dr. Maurice Brooks at the 1978 annual meeting of the Wilson Society.
This became a matter of considerable concern to Wilson members and their officers and Council. We are incorporated in the State of Illinois; each year an official meeting must be held, and a report on organization activities filed with the Secretary of State in that Commonwealth. A goodly number of the officials were in service, many of them overseas and completely out of reach. We had to meet officially or lose our corporate charter, so we began searching for places where travel was possible and where we might come together for essential business matters.

One such place turned out to be the Laboratories of Ohio State University, at Put-in-Bay on Lake Erie. By scraping the barrel, we got enough people for a quorum; thus we fulfilled the law’s requirements and kept ourselves legitimate.

During this war period our sister organizations were experiencing similar difficulties. In the American Ornithologists’ Union there were concentrations of officers and Council members in 4 places—Boston, New York City, Philadelphia, and Washington. Essential business of the Union could be transacted in any one of these.

As a matter of fraternal goodwill, the A.O.U. had officially invited representatives of 2 sister organizations—the Cooper Ornithological Club and the Wilson Ornithological Club—to appoint representatives to sit as members of the Union’s Council. George Miksch Sutton, the Wilson Club’s President in absentia (he was in service), asked me to serve as our Council member at an A.O.U. meeting in New York City.

This was an experience I shall not forget. First of all, I was only an associate of the A.O.U.—not even an elective member at that time. I found myself sitting in small meetings with such people as Robert Cushman Murphy, Alexander Wetmore, Witmer Stone, James Chapin, Frederick C. Lincoln, Herbert Friedmann, William Beebe, and others whose names were celebrated in the outdoor world.

All these men knew each other personally and professionally. They were used to working together on first name basis; practically all of them were Fellows in the A.O.U. And here was I sitting on the Council, an unknown, and merely an associate member of the organization. Such an unheard-of situation could have been embarrassing to everyone concerned. But it wasn’t. Largely through the innate courtesy and kindness of Alex Wetmore, I was made welcome, was extended every consideration, and was made to feel that I was to take part fully in Council’s deliberations. This demonstration of humanness has meant much to me in the years since.

The Wilson Club’s Secretaryship during World War II years carried unusual duties, and unusual opportunities. I had assumed that most persons in service would prefer that their Wilson Bulletins be sent to their homes, there to remain until more settled times. But that didn’t prove to be the case; most of our members in uniform expressed very implicitly the wish that their Bulletins follow them. This, of course, led to a great deal of extra work; it wasn’t unusual to have 2 or 3 address changes for a member in a single year. But from the letters I received it appeared that the Bulletins were a touch of home, a return to normal interests, and a valued element in morale. I still have a file of letters of appreciation.

It soon became evident that the Club could be of additional service to its members. As service personnel began to be placed in all parts of the world, I received increasing numbers of letters from members in uniform who expressed a wish that on free days and leave time they might meet people with bird interests, and might have a chance to get afield in some of the unfamiliar terrain they were occupying. With our international membership, this was usually easy; a letter to a member in New Zealand, Australia, or Great Britain brought cordial response; contacts followed, and many a friendship was established. It wasn’t unusual to have invitations to member’s homes as a part of this.
hospitality; our people abroad were afforded insights that they would otherwise have missed.

When happier times returned and it was again possible to schedule regular meetings of the Club, our first one was held in Omaha, Nebraska, Nov. 28-31, 1946. This was an unforgettable session; emotions were very close to the surface. After 5 long years it was good to be together again.

A major feature of the Omaha meeting was the presence of Nikolaas Tinbergen, visiting America after a long period of involvement in the Dutch underground during Nazi occupation of his homeland. He gave a notable paper at one of the regular sessions, his subject being “The Study of Bird Behavior.” He spoke again informally at the annual dinner, telling of what America’s help to Holland had meant during the dark days of the occupation.

Of course the President spoke, as he always does at such occasions. George Sutton had resumed his interrupted term, and he was at his oratorical best that evening. As many can attest, that is very good indeed, and before he was through there were a lot of damp eyes in his audience. He chose to speak on “Fire,” drawing on his Arctic experiences and what a fire can mean there during the winter months of darkness. He spoke of fire as a guide to safety in the gloom of night, of the flame as a symbol of warmth, comfort, and fellowship. Of course he drew analogies between the Arctic night and the rekindling of the flame in the Wilson Club. It was a moving experience for all who were present. It served to start the Club off with new energy, new goals, and new appreciation for the meaning of its fellowship.

During the next few years there were other interesting developments in the Club’s program. We were affiliated with the American Association for the Advancement of Science, and that organization chose to invite a representative of affiliated societies to sit on the A.A.A.S. Council. I had the opportunity to represent the Club on a few such occasions, and I know that it was a tremendous experience for me. Here were many of the world’s leading scientists, in all fields of scientific endeavor. With them I participated in the business affairs of the Association, listened to arguments, heard plans made for future endeavors in new directions, and felt that I was in the main stream of American science.

When plans were being made for the 1950 meeting of the Wilson Club, I was bold enough to propose a meeting at Jackson’s Mill. I had a precedent for such a country meeting; a year before the American Society of Ichthyology and Herpetology had held a successful meeting at Higgins Lake, Michigan. Persons who attended were loud in their praise of the meeting; they found somewhat primitive conditions a stimulus to informality and productive field work. I knew the possibilities of Jackson’s Mill as a meeting spot; I had been associated with its development since 1922.

Some of our participants arrived with a lot of misgivings. West Virginia, after all, had a national reputation for feuds, coal wars, and abject poverty. They didn’t know what conditions might be facing them.

This is not the time or place to review that meeting in detail. Of one thing I am sure, however; it was an unqualified success. The reluctance to attempt a country meeting was gone for good.

Of course we didn’t play down the Appalachian Mountains image and stereotype. An entertainment feature was a concert by a jug band from the Forestry Division of West Virginia University. Band members chose to appear in straw hats, ragged blue jeans, and no shoes. The wife of one of these men was sitting at a table with 2 ladies from Chicago. She derived great joy when she overheard one say to the other, “I suppose they do have shoes.”
Two years after the Jackson's Mill meeting, we planned another country session, this one at Gatlinburg, Tennessee, in the Great Smokies. There were great anticipations as this meeting approached: after all, the mountains are spectacular, and the biota challenging here in the southeastern outpost of the great trans-continental spruce-fir forest. We had a big attendance, and the meeting was a huge success. It did have one slight hitch; for the 3 days of our sessions there was continuous rain and fog. The mountains never did clear, and a lot of members left without seeing the Great Smokies.

From its early days the Wilson Society has welcomed as fully participating members amateur as well as professional ornithologists. This has been in recognition of the fact that many bird students are amateurs in the truest original meaning of that term. In the past 40 years or so, persons (a lot of them) who are not professionally employed in the field have served as our officers and Council members. So far as I can measure it, this has been of unalloyed benefit to the Society.

It has also been true through the years that the Wilson Society has served as a training ground for officers of the American Ornithologists' Union and other ornithological groups. This, as it seems to me, is highly desirable. Why should trained technical people not make more extensive use of their talents and experience?

As I bring together the memories of 50 years in the Wilson Society, my conviction grows that I would have been infinitely poorer without the contacts that it has afforded. Society-inspired friendships have been warm and lasting. I have not ceased to marvel at the succession of dedicated persons who seem providentially waiting in the wings to take up the responsibilities which the organization must entail. We have seen, and benefited from, a succession of tremendously capable and devoted Editors of The Wilson Bulletin. Our Secretaries and Treasurers have labored to keep our rolls current and our finances sound. So have our other officers, our Council members, our Trustees, and our committee chairpersons. We have been well served by a lot of good people.

And so in closing I choose to return to George Sutton's tribute to fire and its meanings. The Society's flame, kindled 90 years ago, still burns brightly. There is inspiration, warmth and fellowship around its hearth. May this first 90 years be only the happy prologue!

Maurice Brooks
May, 1978
ORNITHOLOGICAL LITERATURE

LAND BIRD COMMUNITIES OF GRAND BAHAMA ISLAND: THE STRUCTURE AND DYNAMICS OF AVIFAUNA. By John T. Emlen. Ornithological Monographs No. 24, 1977; xi + 129 pp. American Ornithologists' Union. $9.00 ($8.00 to A.O.U. members).—For five months each in 1968 and 1969, and during shorter visits in 1971, Emlen censused the birds at 25 sites, representing 22 habitats, on Grand Bahama Island. This monograph is an analysis of the data derived from that field study. Bird censuses were conducted using the Emlen strip-transect technique (Emlen 1971. Auk 88:323–342) and vegetation was sampled on each site using an adaptation of the system developed by Emlen (1956, Ibis 98:565–576).

Grand Bahama, about 100 km off the east coast of Florida, is a low-lying, pine-covered island with an area of 1200 km². Thirty-three land birds (excluding birds of prey) breed on the island and an additional 2 dozen species visit the island as non-breeders during the north temperate winter. About half of the breeding land birds have been derived from the Antilles and one quarter each come from North America and Central America via the Antilles.

The approach is an examination of community patterns at several levels under the following chapter headings: The Habitats and their Bird Communities; Bird Distribution through the Habitats; The Pine-Forest Community—Seasonal Changes; Spatial Distribution within the Pine Forest; and Guild Distribution within the Pine Forest.

Broad scale habitat patterns examined include community composition, structure, diversity, and density. Total vegetation volume was the best predictor of avian diversity. Total bird densities were not well correlated with vegetation volume or insect densities, raising questions about relationships between consumer and resource densities.

Emlen develops models on the dynamics of distribution in winter communities in an effort to account for changing abundances among habitats. On the one hand he suggests that species may be limited solely by the carrying capacity of the environment. Alternatively, he hypothesizes that social intolerance among conspecifics may hold populations below limits imposed by the carrying capacity of the environment. Not surprisingly, aggressive species showed more evidence of a socially saturated plateau than passive species. Further, sedentary species show abundance distributions among habitats similar to those predicted from the hypothesis of social saturation. Thus, the social saturation phenomenon, well-known from breeding season avifaunas, may be common in many species during the winter season.

Species present at high densities in their favored habitats tended to occupy a wide range of habitats, while species with low densities in their favored areas were more likely to be habitat specialists. As in numerous other studies, migrants outnumbered permanent residents in open habitats; for all habitats at least one-third of the individuals in winter communities were migrants.

Most of the monograph is devoted to an analysis of the avifaunas of three pine forest study areas. Seasonal changes in the avifauna were striking from January to June due to the departure of winter residents for North American breeding grounds and the passage of transients which wintered to the south. High densities of winter communities (permanent and winter residents) relative to those of summer communities were not associated with obvious changes in habitat complexity or food availability. Emlen concludes that food supply is "less critical as a limiting factor than commonly supposed" (p. 114). I wonder about the importance of food at other seasons. Or could the non-breeding status, and thus lower energy requirements, of permanent residents in the
winter permit the coexistence of winter residents? Decreased equitability of the winter community results from very high densities of a few wintering species and suggests that only certain guilds might be invasible during the winter.

The last two chapters examine the spatial and guild distribution of birds in the pine forest. Five foliage layers were not equally exploited by birds on the basis of space per se. Not surprisingly, individual species or groups of species showed preference for certain compartments of the habitat. The spatial distribution of permanent residents shifted after the departure of the winter visitors, but the magnitude and direction of the shifts suggests that they are not related to competition between the two groups.

In the final chapter, Emlen describes the guild distribution of pine forest birds. However, his “guild” differs from the traditional foraging guilds so common in the ecological literature in recent years. Emlen apportioned each species’ energy requirements as a fractional proportion of their foraging activities on certain resource types and locations. Emlen’s guild then is the sum of the energy requirements for all part-time as well as full-time exploiters of a specific food resource. Although the approach is not new (see Karr Pp. 161-176 in Golley and Medina (eds.) 1975, Tropical Ecological Systems for another example), the detailed breakdown of Emlen is more sophisticated because it is based on over 1900 observations of foraging activity. Sample sizes seem adequate for many species, but allocation of the Black-throated Blue Warbler among 3 guilds on the basis of 2 foraging observations seems to stretch credibility. However, Emlen deserves praise for rounding to the nearest 10% in contrast to other studies where similar (or less extensive) data bases are used to allocate foraging to the nearest 0.1%.

Emlen sampled insect densities in 5 foliage compartments in an effort to correlate insect abundances with the measured biomasses of birds in the same compartments. No positive correlations were found between food resources and avian consumer densities. This seems a sound approach but I fear that we do not have the ability to index resource densities important to the consumers. What size range of insects is really available (including that energetically exploitable by birds) at any instant in time? Does renewal time alone or integrated with instantaneous density have more significance in regulating community structure? Which season or geographic range is more likely limiting in different consumer groups? Does the importance of these factors change among years? In many respects problems relating to resource density are in their infancy, much like studies of habitat structure before the initial efforts at quantification by MacArthur.

Competition theory, a dominant theme in modern ecology, is both attacked and defended. For example, Emlen seems to invoke competition as the explanation for minimum interspecific overlap of food resources among the ground-gleaning herbivores (p. 94), but rejects competition as an important factor in the interactions of permanent and winter residents (p. 80). I would be happier with an attempt to show why competition is important in one circumstance but not another.

There is considerable food for thought in this monograph, but as is often the case in studies of avian communities, there is room for improvement. Migrants should be viewed not as invaders of a “balanced bird community” (p. 63) but as an integral part of that community. Why should equitability be a good measure of resource sharing (p. 106)? Why should rare residents be classed as visitors because of arbitrary frequency of encounter rules? Such problems of definitions are common in avian community studies. In these and other cases weak inferences are made on the basis of correlations. But this too is a common problem in studies of avian communities. The challenge for the future is the development of stronger tests of specific hypotheses using a manipulative-experimental approach. Emlen and the editors are to be congratulated for providing much of
the raw data in tabular form. They will be valuable long after the "speculations and interpretations in this monograph" are improved or replaced.—James R. Karr.

Water Birds of California. By Howard L. Cogswell, illus. by Gene Christman. University of California Press, Berkeley, California, 1977: 399 pp., 12 color plates, 47 numbered text figs., 2 maps. $5.75—For years the standard treatise on California bird distribution has been the classic The Distribution of the Birds of California by Joseph Grinnell and Alden H. Miller (1944). Although now more than 30 years out of date, it has remained the standard reference primarily because of the authors' careful evaluation of observational records in the literature and their rejection of all unsupported or suspect reports. Several recent authors have attempted to incorporate the vast amounts of data which have accumulated since the publication of The Birds of California. In this reviewer's opinion all such works to date have fallen far short of the mark for one or both of two reasons: either they have tried to reduce the large amounts of information available for each species into a few brief, generalized statements; they have not critically evaluated the data and carefully screened out erroneous and unsubstantiated records; or both.

Water Birds of California is the most recent treatment of bird distribution in California. As with other recent books on the subject, this book is more than merely a distributional analysis. There are sections on behavior, reproduction, and species recognition. Each species' world-wide range, occurrence in California, seasonal status, abundance, and habitat preferences, are also given. Fully one-third of the book (92 pages) is devoted to detailed graphic calendars which incorporate in coded form virtually everything known about each species' seasonal status, abundance, nesting habitats, periods of breeding, and extra-limital occurrences. The introductory chapters deal with subjects that are primarily of interest only to the beginner, such as instructions on how to observe birds in the field, the use of binoculars and telescopes, field note-taking, and identification of birds through the use of picture keys of representative family members. The picture keys, in my opinion, are much more practical than the various color keys, habitat keys, and other such gimmicks so popular in recent field guides that ignore basic taxonomic sequence and family groupings.

Whether or not this book is intended to serve as a field guide is unclear, although the use of color plates, numerous pen-and-ink drawings, and sub-sections on species recognition suggest that this is the intent. Unfortunately many of the birds illustrated are greatly misshapen or in otherwise unnatural positions (see, for instance, the shore-birds in Figs. 28-37 and especially in Fig. 36, and the jaegers in Fig. 38). There are other problems which seriously detract from the usefulness of these illustrations as identification aids. The first-year Double-crested Cormorant in Fig. 8 is all black except for a circle of white on its lower belly. The female Gadwall taking flight in Fig. 18 lacks the conspicuous white speculum. All of the Calidridine sandpipers in Fig. 36 are so badly drawn as to be almost totally beyond recognition. The Pomarine Jaeger in Fig. 38 has a bold black "X" across its back and a head pattern that more closely resembles that of a basic-plumaged Ancient Murrelet. The Craveri's Murrelet in Fig. 46 is actually a Xantus' Murrelet with its pure white under wing coverts. There are many similar examples. With the wealth of talented bird illustrators in California, it is inex-

usable that anyone should feel compelled to publish illustrations of such poor quality.

But what about the text? The book contains much useful information on bird distribution in California, and it is evident that the author (there are no acknowledgments) spent many long hours gathering and organizing the staggering amounts of data available.
in the literature. There is an impressive amount of detailed information in the Graphic Calendars on pp. 300–391 which has been summarized in the species accounts. Unfortunately, the author has used the available data indiscriminately. Many, many records in the published literature are erroneous or insufficiently documented. It is the duty of the compiler of such material to carefully sift through and reject, or query, all such false and suspect material. Because of the misinformation so prevalent in the literature, many commonly held misconceptions have arisen through the years. It is a pity that most recent publications have perpetuated these misconceptions. Most knowledgeable field ornithologists are aware, for instance, that a complete reliance on the literature will result in the false belief that Baird’s and Pectoral sandpipers occur in California in spring and occasionally in winter. Many of these records are the result of misidentifications. A quick look at Water Birds of California revealed the following: Baird’s Sandpiper—“Occ. Rare Nov.–Jan.” (there are no valid records of this species for this period in California), and “Rare to Fairly Common late Mar.–May” (there are fewer than 10 acceptable spring records) [italics are those of the reviewer]; Pectoral Sandpiper—“Irreg. Uncommon or Rare . . . Apr.–May” (there are fewer than 10 spring records); There are many other similar problems throughout the text. For instance, according to the author, the Least Grebe “has nested at least twice and occurs irregularly in very small numbers along the lower Colorado River.” He lists a total of 7 records for this species in the Graphic Calendar. Although all of these are published records, it is commonly acknowledged among field ornithologists in the state that there is only one valid record for this species in California. Another example: “Although the dark phase [of Reddish Egret] predominates in Texas, most of the California records are of the white phase.” The white phase is unknown in the dickeyi subspecies of the Pacific coast.

In general, the author is much too generous in his usage of the terms “abundant,” “very common,” “common,” etc. which he defines on p. 54 as follows: “Abundant = 1000 or more. . . ; Very Common = 250–999; Common = 50–249; Fairly Common = 10–49; Uncommon = less than 10, but frequently more than 3; Rare = 3 or less if Regular, but may be up to 9 if very Irregular.” These categories refer to the number of individuals likely to be seen “in from one-half to one day, in the preferred habitat of that species, during a general search for various birds.” Using these criteria I seriously doubt, for instance, that the Louisiana Heron (p. 100) is “uncommon” in coastal southern California; that the Gadwall (p. 126) is “abundant” in the Central Valley or “very common” in the Imperial and Colorado River valleys; or that the Semipalmated Plover (p. 178) is ever “very common” anywhere in California.

The Graphic Calendars in the appendix are exceedingly difficult to interpret, even after a careful reading of the 12 page introductory material (pp. 287–298). After much flipping back and forth between the calendars and introductory explanations I learned that “1 O, S, IK or IG, OK, U, UB, outer B, nearby dumps, T, c 1 BI >>> 1 inner B, T, nearby L, B, M” for Western Gull distribution translates (I believe) as—ocean and seacoasts: specifically the ocean itself, sandy beaches and flats, rocks, cliffs, and grasslands of islands, and rocky cliffs along the mainland coast, urban areas around piers, buildings, industrial sites, bays, etc.; also outer bays and lagoons, and nearby dumps and tideflats. In central California, coastal bays, estuaries, lagoons and islands, with decidedly less preference for inner bays, tideflats, and nearby lakes, ponds, sloughs, salt-evaporating ponds and other impounded salt water and intertidal salt marshes. Nests on island and mainland seaciffs, grassland areas of islands and in urban bays and estuaries. End of translation. I suspect that most readers will not take the time to wade
through these Graphic Calendars; however, there is a wealth of information available for those who are willing to spend some time decoding them. Unfortunately, as mentioned above, they also contain numerous errors.

This book provides a great deal of information (and much misinformation) about water bird distribution, behavior, and breeding biology in California. The illustrations detract from its appearance and overall usefulness as a field guide, and the numerous factual errors weaken its credibility as a reference book on bird distribution. Nevertheless, it is probably the best single source of information on California water birds to appear since Grinnell and Miller (1944). Let us hope that forthcoming volumes in this series on land birds do not have Swainson’s Hawks and Black-chinned Hummingbirds wintering in California!—H. Lee Jones.

The Audubon Society Field Guide to North American Birds: Western Region. By Miklos D. F. Udvardy, Alfred A. Knopf, New York, 1977: 855 pp. $7.95.—New books sell, especially those lavishly illustrated, regardless of intrinsic merit. This new approach to a field guide, unfortunately, is no exception. There are 3 innovations in this new guide: it departs completely from the phylogenetic arrangement of species, it uses photographs rather than paintings, and the text is arranged by habitats.

The text is well organized, concise, and informative. Udvardy is to be congratulated. The innovation here is in the arrangement of the species accounts by 20 habitat types. The divisions seem excessively fine and might more usefully be reduced to about 5 broader categories that would be less subjective.

Most users will be concerned with trying to identify a bird in the field by means of the photographs. The illustrations are variable in quality. Many are excellent and serve the purpose of field identification well. In particular the long-legged waders, the gull-like birds, the hummingbirds, and the hawk-like birds in flight are useful. Some of the plates are poor. The female Red-shafted Flicker (p. 234) has a golden crown. The White-breasted Nuthatch (p. 242) has blue flanks. Many of the perching birds are shown in such horribly worn breeding plumage or with such distorted colors that one can scarcely guess what species might be represented. Poor choices of abraded summer birds include the Pygmy Nuthatch, Rufous-sided Towhee, Gray-headed Junco, Gray Flycatcher, Mountain Bluebird, Golden-crowned Kinglet, and Bendire’s Thrasher. Some species that should be greenish are figured too gray; all the kinglets, most of the Empidonax flycatchers, and vireos, some of the warblers, and the Green-tailed Towhee. The warblers are mostly too yellow where they should be greenish: Wilson’s, Yellow, Nashville, Townsend’s, Hermit, and Yellow-breasted Chat. But the Scott’s and Hooded Oriole females are far too green. And who could ever identify a female Wilson’s Warbler or Common Yellowthroat from the figures on p. 266?

In a few instances I think better judgement might have been used in deciding what to illustrate. Dendrocoptes woodpeckers, which differ only slightly between the sexes, have separate photos of the males and females. But the Williamson’s Sapsucker, which is so strongly dimorphic that the sexes were originally described as different species, has only the male figured. Misidentifications are few. The “Poorwill” on p. 166 is a Common Nighthawk. A Laughing Gull (p. 67) is called a Franklin’s. The Mexican Duck (p. 108) appears to be a hybrid.

The non-phylogenetic arrangement of illustrations and text probably has about as much to recommend it as does our present archaic sequence of sometimes polyphyletic orders.
In contrast to some of the really satisfactory field guides presently available, I doubt that this one will withstand the test of field use. My copy already has signatures pulling loose from the binding.—Amadeo M. Rea.

Fifty Common Birds of Oklahoma and the Southern Great Plains. By George M. Sutton. University of Oklahoma Press, Norman, 1977: 113 pp., 50 color plates. $7.95—Rarely has the novice been introduced to basic avian biology so expertly and in such a lucid and delightful manner as in this little book (5 × 8¾ × ½ in.). Although the author stresses identification characters such as color, behavior, song, and type of habitat where a species is likely to occur, this book is much more than a beginner's guide. Information relative to each species' eggs, nest, incubation period, enemies, plumages, distribution, and status in Oklahoma is also a part of each description. Personal anecdotes are frequently related from Sutton's rich and varied experiences with birds for more than six decades. These are designed to provoke the reader, whetting his curiosity and inspiring him at every turn to probe a little deeper, learn a little more. Specific problems needing attention are frequently posed. The first line in the description of the Yellow Warbler, for example, is: "The midsummer distribution of this warbler in Oklahoma is puzzling." In the unique Sutton style, ecological lessons are interwoven into the species descriptions. Many plants and animals upon which certain birds depend for one reason or another are alluded to.

Several terms that the author is fond of using are not commonly met in print, for example: alas, rambunctious, frowziness, downright, indeed, meek, and sojourn. Words like these are an integral part of the charm that makes Sutton at once philosopher and raconteur par excellence.

A painting of each species faces its textual description. Some (e.g., Great Horned Owl, Ruby-throated Hummingbird, Redwinged Blackbird) exemplify an earlier, simpler style, and a few are very slightly out of register in my copy, but in general, the quality is exceptionally good. Many in the very audience that Sutton is attempting to reach may have difficulty recognizing the fledgling Blue Jay on page 49. Several plates are especially impressive, particularly the Yellow-billed Cuckoo, Hairy Woodpecker, Western Kingbird, and Dickcissel. It was pleasing to see the Western Meadowlark portrayed rather than the more commonly painted Eastern.

One of the author's greatest difficulties came in choosing which 50 birds to include. Probably no two ornithologists would have agreed on all 50. Better choices might have been the Cliff, rather than the Rough-winged Swallow and the Song, rather than the Lincoln's Sparrow, to name two. However, there is sound reasoning given for selecting each species. But no matter. The author could easily have reached into his vast store of knowledge and plucked out vivid recollections of virtually any Oklahoma bird!

I failed to detect a single typographical error in the text. This is a tribute to the author's meticulous care in proof-reading and to the attention given by the Press during reproduction. The type is clean, bold and large enough to be easily read.

The price might seem a trifle high for a book containing only 113 pages, but the paintings alone are well worth the price.

Many of George Sutton's books go out of print to become expensive, hard-to-find collector's items, attesting to his abiding popularity as writer and bird artist. This book is certain to become the standard primer throughout the region it encompasses, but many ornithologists will regret that it was not available 15 or 20 years ago.—Jack D. Tyler.
CONSTITUTION AND BY-LAWS OF THE
WILSON ORNITHOLOGICAL SOCIETY*

The Constitution and By-Laws of the Wilson Ornithological Society were adopted 29 December 1930, and amended by the Executive Council on 11 August 1945 and 12 June 1975. The revised Constitution and Bylaws were approved by the membership on 29 November 1946, and amended September, 1951 (mail ballot), 9 April 1955, and most recently on 5 June 1976.

CONSTITUTION

ARTICLE I

NAME AND OBJECTIVE

Section 1.—The organization shall be known as the "Wilson Ornithological Society." It shall be registered under that name as a Corporation in an appropriate state, fulfilling any requirements for incorporation under the laws of that state. If the state in which the Corporation is registered should impose new requirements that conflict with the objectives or the financial means of the Society, the Board of Directors of the Corporation may dissolve the Corporation and reincorporate under the laws of another state.

Section 2.—The objective of the Wilson Ornithological Society shall be to advance the science of ornithology and to secure cooperation in measures tending to this end by uniting in a group such persons as are interested herein, facilitating personal intercourse among them, and providing for the publication of the information that they secure.

Section 3.—The official organ of the Society shall be The Wilson Bulletin. It shall be sent to all members not in arrears for dues.

ARTICLE II

MEMBERSHIP

Section 1.—The membership of this society shall consist of five classes: Active Members, Sustaining Members, Life Members, Patrons, and Honorary Members.

Section 2.—Any person who is in sympathy with the objective of this society may be nominated for membership. Nominations and applications for membership shall be made through the Secretary. Applications for membership shall be endorsed by at least one member. Members shall be elected at the annual meeting by a majority of the members present. Nominations presented in the interim between annual meetings shall be received and confirmed by the Secretary, subject to ratification at the next annual meeting.

Section 3.—The Executive Council shall determine the amount of the dues for Active and Sustaining Members, of institutional subscriptions to The Wilson Bulletin, and of payments into the endowment fund of the Society to qualify for the classes of Life Member and Patron. Persons desiring to become Life Members or Patrons may, if they wish, pay one quarter of the amount set for these classes into the endowment fund in four consecutive annual installments. They are then exempt from further dues. Upon the unanimous recommendation of the Executive Council, honorary membership may be conferred by the Society by a three-fourths vote at any annual meeting.

* Incorporated under the laws of the State of Illinois on 16 October 1944.

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Section 4.—All members shall be entitled to vote and to hold office.

Section 5.—All annual dues for the ensuing year shall be due on January 1. Any member in arrears for dues shall be dropped from the roll of members, providing that two notices of delinquency, with an interval of at least two months between them, shall have been sent to such member.

ARTICLE III

Officers

Section 1.—The officers of this society shall be a President, a First Vice-President, a Second Vice-President, a Secretary, a Treasurer, and an Editor. The duties of these officers shall be those usually pertaining to their respective offices.

Section 2.—All officers and elected members of the Executive Council, except the Editor, shall be elected at the annual meeting by ballot of the members. By the unanimous consent of the members, the Secretary may cast one ballot, representing the unanimous vote of the members present. A nominating committee composed of three or more members shall be appointed by the President at the beginning or in advance of the annual meeting, which shall offer nomination of officers and elected members of the Executive Council to serve the Society during the ensuing year. Nominations may also be made by any member in good standing from the floor. The Editor shall be elected annually by the Executive Council.

Section 3.—If no annual meeting can be held, election of officers may be conducted by a mail ballot.

Section 4.—The President and the two Vice-Presidents shall hold office for one year or until their successors are elected, and shall be eligible for re-election for a second year. Upon retirement of the President, the First Vice-President shall be nominated for President and the Second Vice-President for First Vice-President, unless otherwise determined by the Nominating Committee. The Secretary, Treasurer, and Editor are eligible for re-election indefinitely. Terms of office shall begin at the close of the meeting at which the officers were elected.

Section 5.—The officers of the Society, all past Presidents of the Society, and three additional members who shall be elected by ballot of the Society, shall constitute an Executive Council. The term of office for the three elected members of the Executive Council shall be three years without re-election, with terms staggered so that the term of one member expires each year. The Executive Council shall also constitute the Board of Directors of the Corporation. The business of the Society not otherwise provided for shall be in the hands of the Executive Council, which shall pass upon any urgent matters that cannot be deferred until the next annual meeting. Five members of the Council shall constitute a quorum.

Section 6.—Vacancies in the staff of officers, occurring by death, resignation, or otherwise, shall be filled by appointment of The Executive Council, but the person so appointed shall hold office only until the close of the next annual meeting of the Society, except in event of his election to that office by members of the Society.

ARTICLE IV

Meetings

Section 1.—The Executive Council shall determine the time and place of regular annual meetings of the Society.

Section 2.—Twenty-five (25) members shall constitute a quorum for the transaction of business at regular annual meetings.
ARTICLE V

Accounts

Section 1.—A committee shall be appointed annually by the President to audit the accounts of the Treasurer.

Section 2.—The proper care of an Endowment Fund shall be provided for by a Board of Trustees. This Board shall consist of three members appointed by the President.

ARTICLE VI

Amendments

Section 1.—This constitution may be amended at any regular annual meeting by two-thirds vote of the members present, provided that the amendment has been proposed at the preceding annual meeting or has been recommended by a two-thirds vote of the Executive Council, and a copy has been sent to every member of the Society at least one month prior to the date of action.

ARTICLE VII

Bylaws

Section 1.—Bylaws may be adopted or repealed at any annual meeting by a majority vote of the members present, provided that a copy of the suggested changes has been mailed to every member of the Society at least one month prior to the regular annual meeting.

BYLAWS

1. Notice of all meetings of the Society shall be sent to all members at least one month in advance of the date of the meeting.
2. The time and place of the business session shall be published prior to the opening session of the annual meeting.
3. A scientific program committee and a local committee on arrangements for the annual meeting shall be appointed by the President at least ninety days in advance of the meeting.
4. A committee on resolutions shall be appointed by the President at the beginning or in advance of the annual meeting.
5. The accumulation and care of a Wilson Ornithological Society library shall be provided for. A library committee shall be appointed annually by the President.
6. The Executive Council shall have power to expel any person found unworthy of membership in the Society.
7. The fiscal year of this Society shall be the calendar year.
8. The agenda at regular annual meetings shall include:
   a. Calling of meeting to order by the President.
   b. Reading and approval of minutes of the previous meeting.
   c. Reports of officers.
   d. Appointment of temporary committees.
   e. Election of members.
   f. Business.
   g. Reports of committees.
h. Election of officers.
i. Adjournment.

9. The rules contained in Robert's Rules of Order shall govern the Society in all cases to which they are applicable and in which they are consistent with the Constitution and Bylaws of the Society.

10. This constitution and bylaws may also be amended by mail ballot provided that the amendment has been recommended by a two-thirds vote of the Executive Council, and a copy has been sent to every voting member of the Society at least two months prior to the date of action.
ORNITHOLOGICAL NEWS

1979 ANNUAL MEETING

"The Wilson Ornithological Society will hold its annual meeting at the University of Nebraska at Omaha, Nebraska, on 4-8 April 1979. We will be the guests of the University of Nebraska at Omaha and the Nebraska Ornithologists' Union. Information regarding lodging and field trips and abstract forms for submitting papers will be mailed to the membership early in 1979. The meetings will include sessions for contributed papers and a symposium dealing with the biology of avian species that have restricted ranges. Because of the early 1979 meeting, the deadline for submission of abstracts will be 15 February 1979."

WILSON SOCIETY MEMBERSHIP ANNOUNCEMENT

The Wilson Ornithological Society cordially invites all individuals who are interested in birds to join the society. Founded in 1888, the society prides itself in the way both amateur and professional ornithologists take an active part in its organization and operation. Dues are $14.00 for regular members and $10.00 for students. Life Memberships can be obtained until 31 December, 1978, for $200.00. For information and application forms, please write Robert C. Whitmore, Membership Chairman, Wilson Ornithological Society, Division of Forestry, West Virginia University, Morgantown, WV 26506.

W.O.S. CONSERVATION COMMITTEE: FEDERAL BIRD PERMIT STUDY

Ornithologists experiencing difficulties securing federal collecting and related permits in recent years are asked to outline their problems with full documentation for action by the WOS Conservation Committee. Of special interest are those instances where the permit process hampered scientific research. Please send details at once to the Committee’s Chairman, Eric G. Bolen, c/o Welder Wildlife Foundation, P. O. Drawer 1400, Sinton, Texas 78387.

NOTICE TO CONTRIBUTORS

Effective immediately, new manuscripts to be considered for publication in the Wilson Bulletin should be sent to editor-elect, Dr. Jon Barlow, Department of Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6. Correspondence concerning volume 90 of the Wilson Bulletin should be sent to the present editor.

This issue of The Wilson Bulletin was published on 21 November 1978.

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Suggestions to Authors

See Wilson Bulletin, 87:144, 1975 for more detailed "Suggestions to Authors." Manuscripts intended for publication in The Wilson Bulletin should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411-419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in “General Notes” should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the “CBE Style Manual” (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

Notice of Change of Address

If your address changes, notify the Society immediately. Send your complete new address to the Treasurer, Ernest E. Hoover, 1044 Webster St., N.W., Grand Rapids, Michigan 49504. He will notify the printer.

The permanent mailing address of the Wilson Ornithological Society is: c/o The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

* See Ornithological News, p. 478, for address for ms submission.
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Allen Press, Inc., Lawrence, Kansas 66044
Male Thayer's Gull (Larus thayeri) about three and one half years old drawn direct from life by George Miksch Sutton on 15 March 1966. Captured while still a downy chick in August, 1962, on one of the Finlayson Islands, in the Canadian Arctic Archipelago, the bird was reared in captivity.
ON MATURATION OF THAYER’S GULL

GEORGE M. SUTTON AND DAVID F. PARMELEE

The New World arctic larid known as Thayer’s Gull (Larus thayeri) resembles the well known, widely distributed Herring Gull (L. argentatus) in so many ways that some taxonomists believe it to be a geographical race of that species. Although we have long entertained the belief that a fairly close taxonomic relationship exists between thayeri and argentatus, substantiated in part by the studies of Smith (1966), we also recognize the possibility that thayeri may, in view of recent findings by Earl Godfrey (pers. comm.), be conspecific with the Iceland Gull (L. glaucoides). No doubt many aspects of all these birds’ lives, including maturation, need to be explored in depth. Until Godfrey’s findings are published, however, we find it expedient to compare thayeri with argentatus at this time.

The plumages and molts of thayeri and argentatus appear to be much the same. The careful student cannot help suspecting, however, that identification of thayeri under 4 years of age has been guesswork. This being possible, we decided—while based at the village of Cambridge Bay, Victoria Island, in the Canadian Arctic Archipelago, in the summer of 1962—to capture and rear some young Thayer’s Gulls; to photograph them from time to time as they developed; and to preserve the rectrices of at least one individual, set by set, so as to ascertain what the tail of a maturing bird of known parentage actually looked like. Our decision resulted in part from realization that a small but thriving colony of thayeri nested on one of the Finlayson Islands about 48 km southwest of Cambridge Bay.

SPECIMENS AND METHODS

The colony occupied a cliff on one of the larger islands of the Finlayson Archipelago. Glaucous Gulls (L. hyperboreus) nested on the same island, more or less colonially, but above and to one side of the thayeri colony. Parmelee had visited the Finlaysons on 21 June 1960, finding eggs in all of the 19 thayeri nests that he examined. On 3 June 1962, the 2 of us travelled to the islands by dogsled over the sea ice, finding about 30 Thayer’s Gulls and about 50 Glaucous Gulls at the colony-site. On 10 August 1962, Sutton and H. A. Stephens, taken to the colony in the motorboat Spalding by Corporal R. I. Fendrick and Special Constable Andrew Iyago of the Royal Canadian Mounted
Police, counted 41 adult *thayeri*, collected one adult female, and captured 7 fairly large but still downy chicks, 2 of which they preserved as skins the following day (Parmelee et al., 1967:159-160).

To the surprise of their captors, the 5 young gulls that were kept alive were far from omnivorous. They preferred fresh fish and fresh meat to any other food. Their disdain for cooked mixtures of oatmeal and powdered eggs was puzzling and exasperating. They loved to bathe and "play" in water furnished them in a dishpan. The flight from Cambridge Bay to Edmonton, Alberta, and the drive from Edmonton to Kansas must have been hard on them, but they survived it all; they adjusted readily to life in a flight cage at the zoo in Great Bend, Kansas; and there some of them probably would be today had one not been "collected" on 15 March 1966, when it was 3 years and 8 months old (direct-from-life drawing made, skin preserved), and had not a mink killed the remaining 4 one year later (31 March 1967). Two of the 4 mink victims were virtually demolished: the skins of the other 2 were preserved.

The fact that the plumage of the caged birds continued to be in good condition and that the birds fared well in captivity merits emphasizing. They did not seem to suffer from the heat even during the summer when extensive molting took place each year.

RESULTS AND DISCUSSION

Color of eyes and eyelids.—Adult *thayeri* and *argentatus* differ considerably, and consistently, in eye-color and eyelid-color. Eyes of adult *thayeri* are of 2 sorts, light and dark. In light-eyed birds the irides are pale yellowish gray or pale brownish gray, clouded with highly variable, unevenly distributed, fine dark speckling. In dark-eyed birds the irides are deep, rich brown, almost black, and without speckling. In adult Herring Gulls the irides are invariably "very pale lemon" yellow (Witherby et al. 1948:93).

Whether adult *thayeri* are both light-eyed and dark-eyed throughout the range of the species remains to be ascertained. We certainly observed both light-eyed and dark-eyed birds in 1962 and 1966 at Cambridge Bay. Smith (1966) presumably observed both in all *thayeri* colonies visited by him in 1960 and 1961. But "all adult" specimens taken by Macpherson at Pelly Bay "had irides more or less speckled with brown or dark gray" (Macpherson 1961:21); and a sketch made on 15 August 1923, by J. Dewey Soper of a bird taken at Dundas Harbor, North Devon Island, a sketch made on 31 July 1929 by Percy A. Taverner of a male taken at the same locality, and sketches made by J. A. Crosby of 3 specimens taken at Resolute Bay on 28 August, 30 August, and 1 September 1954, are all of light-eyed birds—facts justifying a suspicion that dark-eyed birds may be absent from, or rare in, some parts of the species' range.

Dark-eyed *thayeri* are recognizably dark-eyed in the field, even at considerable distance. In late August and early September, 1962, Sutton and H. A. Stephens saw about equal numbers of light-eyed and dark-eyed adult birds at Cambridge Bay. Of 9 adults captured by them in padded steel traps
near their tent, 5 were light-eyed and 4 dark-eyed, and none of the 9 had light-and-clear irides or dark-and-speckled irides. The 5 chicks reared by them had fairly light brownish gray eyes until they were about 2½ years old: at that time 3 became increasingly light-eyed and 2 increasingly dark-eyed: but while they were held captive at Great Bend, Kansas (1 October 1962 to 31 March 1967), none of the 4 that were not sacrificed became as light-eyed or as dark-eyed as the fully adult individuals color-photographed at Cambridge Bay in late August and early September, 1962.

Eyelids of \textit{thayeri} a year old or older are reddish flesh-color or purplish flesh-color, while those of adult \textit{argentatus} have been described as “from dull straw-yellow to bright yellow-orange” (Sutton 1932:180); as cadmium yellow, cadmium orange, and deep chrome (Macpherson 1961:24); and as “orange” (Smith 1966:6, and frontispiece; Witherby et al., \textit{loc. cit.}). We find very little concise information on the eyelid-color of Herring Gulls 2 to 4 years of age: Witherby et al. (\textit{loc. cit.}) state that it is “pink-brown” in young birds up to their third winter.” Less-than-one-year-old \textit{thayeri} and \textit{argentatus} may, we believe, resemble each other closely as regards iris-color and eyelid-color.

\textbf{Nest site preference.}—Thayer’s Gulls nest on cliffs, usually along the outer coast, and as a rule colonially (Manning et al. 1956:96; Parmelee and MacDonald 1960:62; Macpherson 1961:19; Smith 1966:6), whereas Herring Gulls almost never nest on cliffs and often do not nest colonially. In southern Southampton Island, in 1930, \textit{argentatus} nested chiefly in separate pairs on boulders “in the middle of the tundra” or on “little rocks in the lakes,” but also to some extent, in small loose colonies (Sutton 1932:173–179). In 1955, in the vicinity of Cape Dorset, southwestern Baffin Island, \textit{argentatus} nested principally in scattered pairs “on boulders in lakes,” though “three colonies were found on small islands in lakes” (Macpherson 1961:22). Neal G. Smith, who, in his study of 4 arctic gulls, paid special attention to nest-site preference, found \textit{argentatus} nesting in scattered pairs and ill-defined colonies in “tundra valleys and flat marshy regions” at Cape Dorset in 1959; in “flat marshy” country in the “Frozen Strait” area [Southampton, Coats, and Vansittart islands and southern Melville Peninsula], in 1960; and in “small numbers on deltas at the heads of fjords” near Home Bay, on the east coast of Baffin Island, in 1961 (Smith 1966:24–29).

Where \textit{thayeri} and \textit{hyperboreus} coexist in a vast area where \textit{argentatus} does not occur, \textit{hyperboreus} breeds commonly on both cliffs and tundra ponds. But where \textit{argentatus} breeds on tundra ponds, \textit{hyperboreus} confines its nesting mostly to cliffs.

\textbf{Natal plumage of \textit{L. thayeri}.}—According to Manning et al. (1956:100, footnote), the downy chick of \textit{thayeri} has “more white on the breast and belly, slightly less distinct spotting, and slightly less buffy tinting on the back” than
the chick of argentatus. These authors continue: "It is doubtful, however, if all the individuals in a mixed series could be correctly separated." Macpherson (1961:31) states that the downy chick of argentatus is "slightly more buffy" that that of thayeri.

We have not seen a living newly hatched thayeri. We have, however, examined 3 small chicks in the collection of the National Museums of Canada, specimens taken by A. H. Macpherson at Pelly Bay on 4 August 1956. These and the 2 older chicks taken by Sutton and Stephens on the Finlayson Islands on 10 August 1962 (see above), differ enough inter se to suggest that in thayeri there is just as much individual variation in the intensity and distribution of the dark dorsal spotting as there is in the natal plumage of argentatus. The 5 just-mentioned thayeri prove to be virtually indistinguishable as a group from 5 downy argentatus (1 from Great Slave Lake, 1 from Southampton Island, 3 from James Bay) lent by the Carnegie Museum. The thayeri are a trifle grayer throughout and a trifle paler below than the argentatus, thus agreeing with the descriptions of Manning et al. and Macpherson. The buffiest individual of the 10 is an example of argentatus (CM 40064) taken 7 July 1912, at Way Rock, Rupert Bay, James Bay, by W. E. Clyde Todd. That this buffiness is not the result of foxing is evident from the fact that 2 older specimens taken in James Bay in 1912 (CM 40260, 40261) are not by any means as strongly buffy in tone. Unfortunately there are no comments concerning the colors of fleshy parts on any of the 10 original labels.

Winter plumage of L. thayeri.—Two young male thayeri taken by Sutton at Cambridge Bay on 6 and 7 September 1962 (GMS 14489, 14490), are in either juvénal or first winter feather. Neither was molting. As prepared specimens they are much like, but paler than, a young Herring Gull taken from a colony of argentatus on the Marblehead Rocks near Marblehead, Essex County, Massachusetts, by W. H. Drury, Jr., on 31 August 1965. Whether the 3 specimens are strictly comparable is a question. The Herring Gull is obviously very young, for natal down still clings to some plumage of the head and neck, and the rectrices and remiges are sheathed at the base. Judging from the fact that our captive thayeri molted no feathers at all in their cage at Cambridge Bay, and very few in their carrying cage while being transported to Kansas, clearly shows that their postjuvenile molt did not start until after 29 September. This being the case, the 2 "wild" specimens above referred to were probably in juvénal rather than first winter feather. While we continue to feel that thayeri in its first winter feather may be grayer (less brown) than argentatus of the same age, we have no proof of this. The paleness of the 2 thayeri is, however, quite apparent: it is noticeable throughout the plumage as a whole in both specimens: and it is especially noticeable in the remiges, rectrices, and dark
parts of the dorsal body plumage. The 5 “juvenal” \textit{thayeri} pictured by Macpherson (1961:plate 4) are, on the whole, paler than the 4 “juvenal” \textit{argentatus} pictured in the same plate. The extent and timing of the postjuvenal molt in \textit{thayeri} remain to be ascertained.

The winter plumage of fully adult \textit{thayeri} differs from the breeding plumage chiefly in that the white of the head and neck is streaked with grayish brown. In this respect \textit{thayeri} resembles \textit{argentatus} closely. Whether \textit{thayeri} under 2 years of age have a summer plumage that is distinguishable from their winter plumage is doubtful: birds up to about 2 years of age are, in other words, more or less streaked on the head and neck at all seasons. Photographs taken of our captives on 26 June 1965 (birds just under 3 years of age), however, show the head and neck to be pure white. Photographs taken on 12 March 1966 (birds about 3½ years old) clearly show all to be streaked on the head and neck, “902” and “903” much more so than the others, “904” decidedly the most heavily of the 5 (see frontispiece).

\textit{Changes in rectrices}.—Realizing that tail feathers molted normally would be frayed, faded, soiled, or lost, we decided to pull and preserve the rectrices of one of our captive birds at least once a year until a white tail came in. Our assumption that only one of the annual molts would normally be extensive enough to include the tail: that only 3 tails would normally be worn and molted before a fully white tail came in; and that these first 3 tails would show a gradual change from dark gray to pure white, was based on our long-standing belief that such a maturation procedure had been fully documented for the Herring Gull (see Dwight 1920, 1925; Poor 1946). We now believe, however, that no one, not even Dwight or Poor, has studied, compared, and photographed or drawn Herring Gulls of known age continuously in an attempt to ascertain exactly how many partly dark tails are worn before a fully white one comes in. The excellent figures in Dwight may well have been drawn from birds believed, rather than known, to be of a certain age: and Poor’s careful studies reveal that “many fourth year birds” do not have pure white tails (Poor 1946:150).

In any event, we pulled and preserved 7 partly dark tails (Fig. 1) from captive \textit{thayeri} “903” (band no. 567-81903) and 4 extensively dark tails from “905” (Fig. 2) before either bird was 4 years old; and “904,” photographed on 29 July 1965, had a very dark tail on that date and a still partly dark tail 5 months later (on 11 December 1965) when approximately 3 years and 5 months of age (Fig. 3). This bird was wearing the same, or virtually the same, “partly dark tail” when it was sacrificed on 15 March 1966. On that date 1 rectrix was pure white, a circumstance strongly suggesting (though not proving) that a pure white tail was coming in at last. We have no way
Fig. 1. Eight tails of captive male Thayer’s Gull “903.” Tails 1–7 were pulled between 27 October 1962 and 9 October 1964, well before the bird was 4 years old. Tail 8, worn by the bird when it was killed by a mink on 31 March 1967, was pure white—like the tail that directly followed tail 7.

of knowing whether there was one white rectrix in the tail on 11 December 1965: no such rectrix clearly shows in the photograph.

We continue to believe that in thayeri as well as in argentatus only one molt per year involves complete replacement of the remiges and rectrices. We cannot, however, offer proof of this. What we do know, from comparison
Fig. 2. Four tails of captive female Thayer’s Gull “905.” Each of these was pulled at one “sitting” (on 24 October 1963; 10 January 1964; 9 April 1964; and 9 October 1964) well before the bird was 3 years old.

of the very dark tail of “904” photographed on 29 July 1965, with the largely white tail worn by the same individual on 11 December 1965 (photograph taken) and on 15 March 1966 (specimen preserved), is that the change from dark to light tail can be swift and striking (see Fig. 3). We are reasonably sure that the “very dark tail” in this case was replaced directly by the “largely white” tail, for it is virtually unthinkable that a wholly different set of rectrices came in and dropped out during the 5-month intervening period. It is also important to note that this molt was natural and not the result of plucking.

Individual variation in the rate at which rectrices are replaced may be very great in thayeri less than 4 years old. The “very dark tail” of “904” was photographed 29 July 1965, as stated above; on the same date Tail 7 of “903” was very nearly white (see Figs. 1 and 3). It can be argued, of course, that we are reporting on an abnormal situation because “903’s” tails were plucked several times; but we feel that our findings, inconclusive though they may be, should be reported.

The first 7 tails of “903” (Fig. 1) were pulled during the first 3 years of the bird’s life. Tail 1 was pulled 3 feathers at a “sitting” between 27 October and 9 November 1962; Tail 2 three feathers at a “sitting” between 12 January and 4 April 1963; the other 5 tails at one “sitting” each respectively on 23 October 1963; 10 January 1964; 9 April 1964; 9 October 1964; and 1 August 1965. The pure white rectrices of Tail 8 were pulled from what
was left after the mink massacre of 31 March 1967. Three of the inner rectrices of Tail 3 are noticeably shorter than the 5 darker ones to their left. These shorter ones were slightly browner (less gray) than the others, too: they developed from papillae that produced the last 3 feathers pulled from Tail 2 on 4 April 1963.

Changes in primaries.—We decided against pulling major wing feathers partly because these proved to be very hard to pull. The primaries of all 5 captives during their first year were grayish brown, without obvious patterning. Four inner primaries pulled from “903” on 12 February, 17 February, 20 March, and 12 April 1963, respectively, were somewhat darker on the outer web and at the tip than throughout most of the proximal part of the inner web, and they had only a faint hint of subterminal patterning.

We do not know exactly when these first primaries were molted. The
primaries of 2 birds photographed 9 October 1964, were patterned at the tip, but neither the black nor the white was bold. These primaries were probably of the birds' second set. The wing of "903" photographed in February, 1965, shows what was probably the third set of primaries. These have rather bold black patterning but only a suggestion of white—this being the outermost and on the fifth and sixth, counting from the outside (see Fig. 4). Again we must call attention to individual variation: the primaries of "905," photographed that same day, show no white at all. The boldness of black patterning in "903" could not have resulted from pulling of feathers in the spring of 1963 (see above), for those primaries were pulled from the right wing, and the wing photographed was the left.
The inner primaries of "904," photographed 29 July 1965, when the bird was about 3 years old, were boldly tipped with black and white—the pattern being that of the fully mature bird. When this bird was sacrificed 3½ months later, all its outer primaries were boldly patterned with black and white at the tip despite the fact that its tail was not yet free of subterminal dark markings. We believe that "904" (GMS 14938) is wearing its fourth set of remiges (Fig. 5).

Assumption of pale gray mantle.—Gulls "903" and "905," photographed several times on 23 October 1963, had no gray feathers in the back plumage, scapulars, or wing coverts (see Fig. 6). These birds were about 15 months old, so their body plumage almost certainly had undergone at least one complete replacement. Just how old the birds were when the gray mantle plumage began to appear, and how old they were when this first gray mantle became complete, we do not know: but all 5 birds, when photographed 24 October 1964, when about 27 months old, had gray mantles.
Fig. 6. Captive Thayer’s Gulls about 15 months old, photographed at zoo in Great Bend, Kansas, 23 October 1963. The gray mantle has not yet appeared.

Changes in bill color.—We made no attempt to write down notes on observed changes in bill-color, but colored photographs taken in August and September, 1962, October, 1963, October, 1964, and February, 1965, all show the bills of the captives to be brownish gray (darkest during the first year), without any tinge of yellow, with a dark subterminal area on both maxilla and mandible, and a hint of pinkish flesh-color at the base of the mandible. By 29 July 1965, when Parmelee sketched “902” in watercolor, the bill had become yellow and an orange-red spot had appeared near the tip of the mandible of this 3-year-old bird. On this date a large dusky subterminal spot remained on the maxilla and a small one on the mandible. Kodachromes of “904” and “905” taken 11 December 1965, show the bill to be definitely yellow, with a greenish cast; they also show reduction in size of the dark subterminal spot on both the maxilla and mandible. By 15 March 1966, when Sutton painted and killed “904,” the bill was decidedly yellow, the dark subterminal area had largely disappeared, and the orange-red mandibular spot was clearly evident (see color-plate). The patterning of the bill is fairly evident even in the preserved skin.

COMMENTS

Let it be clearly understood that we have not argued that maturation requires more time in *Larus thayeri* than it does in *L. argentatus*. Ascertaining how many sets of rectrices normally are worn and dropped before pure white
rectrices come in will require careful further work over a 4- or 5-year period. Variation in iris-color of \textit{thayeri} should be investigated thoroughly. Parmelee's observations of a dark-eyed subadult captive on 29 July 1965, convinced him that the iris became noticeably darker (and the pupil larger) when the bird was moved from sunlight into shade. Dark-eyed, fully adult, wild birds observed by Sutton at Cambridge Bay in August and September, 1962, were very dark-eyed in full sunlight, where they were photographed (see color-plate). Fully adult \textit{thayeri} should be observed throughout the year to ascertain to what extent the color of irides, eyelids, and bill may vary seasonally.

ACKNOWLEDGMENTS

We wish to thank W. Earl Godfrey of the National Museums in Ottawa for letting us examine field sketches of \textit{thayeri} made by P. A. Taverner, J. D. Soper, and J. A. Crosby, and for lending downy chick specimens of \textit{thayeri}; Corporal R. I. Fendrick and Special Constable Andrew Iyago of the Royal Canadian Mounted Police for helping Sutton and H. A. Stephens to capture the 7 gull chicks on the Finlayson Islands; Kenneth C. Parkes of the Carnegie Museum in Pittsburgh for lending specimens of downy chick \textit{argentatus}; William H. Drury, Jr., for furnishing us with an unskinned \textit{argentatus} in juvenile feather; John S. Weske for preparing the skin of this specimen; Paul S. Nighswonger for photographing the tails of some of the captive birds; David M. Niles of the Delaware Museum of Natural History for photographing the wingtips of one specimen; and Jean M. Parmelee for typing the final copy of the manuscript.

LITERATURE CITED


REQUESTS FOR ASSISTANCE

A list of birds that eat salt is being prepared. Correlations will be sought taxonomically, between seasons, habitats, condition of the birds (breeding or non-breeding), etc. Any reprints or unpublished accounts would be appreciated. Please send to Kathryn Herson, Biology Department, Western Michigan University, Kalamazoo, MI 49008.

Double-crested Cormorant.—Information is requested on sightings of color marked Double-crested Cormorants. Birds are marked with standard USFWS aluminum leg bands plus colored vinyl leg streamers, on either one or both legs. Data requested: Color and location of streamer, single letter code if possible, date and exact location of sighting. I am especially interested in sightings from wintering areas. Please advise Bird Banding Laboratory, Office of Migratory Bird Management, Fish and Wildlife Service, Laurel, MD 20811 and/or Marcella M. Bishop, Shoreline Route, Polson, Montana 59860.
Do birds merely cope with pack ice as a physical barrier restricting access to the sea and its food resources, or are they so adapted to exploit the opportunities it presents that they rely on its presence? The answer to this question would greatly further our understanding of seabird community organization in polar regions. After all, pack ice is unique to polar seas and several seabird species are unique to pack ice regions, particularly in the Antarctic (see Murphy 1936).

The first steps toward understanding the relationship of seabirds to Antarctic pack ice are to document bird occurrence under various ice conditions and to determine whether seasonal changes in ice cause changes in the bird life. Because ice hinders ship travel our knowledge of bird occurrence in the Antarctic is limited, especially in the Ross, Bellingshausen, and Weddell seas where the pack ice is heaviest and most persistent (see summary in Watson et al. 1971). Shipboard censuses have been sporadic and have largely taken place in late summer when ice conditions are lightest. Only the observations by Cline et al. (1969), made during late summer in the Weddell Sea, offer much insight into Antarctic bird/ice relationships, and only those by Parmelee et al. (1977), taken in a relatively ice-free area of the Antarctic Peninsula near the periphery of Antarctica, offer information on seasonal changes in the Antarctic avifauna. The present paper adds to this knowledge by summarizing information gathered during 12 periods, early spring to fall (1962–1976: Table 1), at Cape Crozier, Ross Island, in the Ross Sea at virtually the southernmost reach of the ocean (Fig. 1).

STUDY AREA AND METHODS

Cape Crozier is at the juncture of Ross Island, the Ross Ice Shelf and the most southerly portion of the Ross Sea (Fig. 1). Each year during the periods of 1961–1971 and 1974–1976, we travelled by helicopter or by overland traverse from McMurdo Station about 70 km away. Once at Crozier our stay was continuous, usually from mid-October to mid-February (Table 1). Each season we visited the Emperor Penguin (Aptenodytes forsteri) rookery which is about 5 km from the field camp. Until 1970–71 the bird log kept by Wood contained all records of the less common species but only irregular sightings of the common ones. All persons at Crozier were invited to contribute observations and emphasis was placed on recording the first sighting of each species each season. In the last 2 seasons Ainley maintained a daily log of all birds seen as well as the number of hours spent in observation. During the 10 to 12 h spent in the field each day, the sea was searched for birds every 3 to 10 min. Each day that the wind was below 88 km/h at least 1 continuous hour, often more, was spent scanning
the sea from a good vantage point on the beach 10 m above the sea. From there, birds could be detected within about 2 km. Beginning in the 1967-68 austral summer (excepting 1970–71), daily records were kept of wind speed and direction (measured by an anemometer and wind vane) and percent of ice cover on the seas visible from the hut. We could usually see pack ice conditions 40 km out to sea from the hut at 135 m elevation; a new hut replaced the old one in 1974, but ice observations were still recorded from the old site.

**SPECIES ACCOUNTS**

**Emperor Penguin** (*Aptenodytes forsteri*).—The Cape Crozier Emperor Penguin breeding colony, the southernmost and the first discovered for this species, is one of the smallest in population size. Adults arrive to nest in late June, eggs laid are incubated from late June through August and chicks hatch in September. This schedule is about a month later than at more northerly rookeries (see summary in Stonehouse 1953). By mid-December the earliest hatched young fledge and by early January all birds have de-
### Table 1
**Dates on Which Species Were First Sighted at Cape Crozier During Each Summer Period**

<table>
<thead>
<tr>
<th>Observation Period</th>
<th>Chinstrap Penguin</th>
<th>Snow Petrel</th>
<th>Antarctic Petrel</th>
<th>Southern Fulmar</th>
<th>Giant Petrel</th>
<th>Wilson's Storm-Petrel</th>
<th>Brown Skua</th>
<th>Southern Black-backed Gull</th>
</tr>
</thead>
<tbody>
<tr>
<td>16 Oct 1962–2 Mar 1963</td>
<td>24 Feb 17 Nov 26 Dec</td>
<td>8 Jan 23 Dec</td>
<td>8 Jan 6 Jan 9 Jan</td>
<td>2 Dec 4 Dec mid-Nov</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20 Nov 1967–14 Feb 1968</td>
<td>? 7 Dec 19 Dec 10 Jan 11 Jan 12 Dec</td>
<td>2 Dec</td>
<td>4 Jan</td>
<td>?</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20 Oct 1968–16 Feb 1969</td>
<td>15 Nov 2 Dec</td>
<td>4 Jan</td>
<td>2 Dec</td>
<td>4 Jan</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>23 Nov 1970–21 Dec 1971</td>
<td>(3 Dec) 3 Dec 17 Dec</td>
<td>18 Dec</td>
<td>2 Dec 4 Dec (not seen)</td>
<td>19 Dec</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

— Observation period inappropriate to determine valid first date.
( ) Date possibly affected by period of observation.
? Present but no notes on date of first sighting.
### Table 2

**Count-estimates of Emperor Penguins at Cape Crozier, Ross Island**

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of adults</th>
<th>Number of chicks</th>
<th>Number of breeding pairs</th>
<th>Dates of observation</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>1967</td>
<td>500±</td>
<td>0</td>
<td>?</td>
<td>19 Oct</td>
<td>About 200 adults seen wandering in pack-ice off Adélie rookery</td>
</tr>
<tr>
<td>1968</td>
<td>1000±</td>
<td>651 (60)</td>
<td>711</td>
<td>26 Oct, 16 Nov, 1 &amp; 6 Dec</td>
<td>Two separate breeding groups</td>
</tr>
<tr>
<td>1969</td>
<td>1300±</td>
<td>680 (17)</td>
<td>697</td>
<td>23 Oct, 11 Nov, 2 &amp; 22 Dec³</td>
<td>One breeding group</td>
</tr>
<tr>
<td>1974</td>
<td>600±</td>
<td>249 (7)</td>
<td>256</td>
<td>14 Nov, 17 Dec,² 31 Dec³</td>
<td>One breeding group 200 m back from the sea</td>
</tr>
<tr>
<td>1975</td>
<td>274</td>
<td>94 (24)</td>
<td>108</td>
<td>29 Oct,² 18 Nov,⁴ 5 Dec³</td>
<td>Breeding group 500 m back from the sea. Many adults wandering in pack-ice off Adélie rookery</td>
</tr>
</tbody>
</table>

¹ Numbers in parentheses in chick column are of dead chicks.
² Derived by adding number of live and dead chicks; minimum estimate.
³ Observations made from cliffs above rookery.
⁴ Visit made at sea level but no entry made into vicinity of breeding group.

Thus our observations which began in October each year cover only the last third of the Emperor breeding season.

In 1962 and 1963, Stonehouse (1964) estimated 1500 breeding pairs at Cape Crozier, a population 4 to 5 times greater than 60 years earlier (Wilson 1907). He attributed the change to an increasingly favorable breeding environment brought about by movement of the Ross Ice Shelf against the Ross Island cliffs. During October and early November, 1968 and 1969, we estimated a population of 720 breeding pairs based on our counts of chicks (including dead ones; Table 2). In 1974 and 1975, we estimated 260 and 120 breeding pairs, respectively. With the exception of 1967 (see Table 2), every population estimate since 1962 has been lower than the previous count.

Apparently unfavorable nesting habitat contributed to the low numbers in 1975. Other unknown factors such as fewer breeding adults may also have been involved but we were not present at egg laying and can not be sure. The colony was situated 500 m back from the sea and was accessible only over a very tortuous route with many crevasses. The route was so difficult that we quickly gave up attempts to follow it and instead censused chicks...
from the cliffs directly above. Although we made a thorough search of more accessible areas, we found no evidence of other nesting birds. Open water occurred right to the edge of the ice shelf instead of, as in other summers, there being fast sea ice upon which the birds reared young. Conceivably they bred on this ice in 1975, but as in 1902 and 1967 (see Wilson 1907, Stonehouse 1964, Sladen et al. 1963) an unusual storm may have broken the ice loose and swept the birds to sea. Unusually large numbers of adults wandered about over the pack ice off the Crozier Adélie rookery during both 1967 and 1975, and during both years far more than usual numbers of Emperors were seen as far away as McMurdo Station. These birds were quite possibly ones that had failed to breed or failed during breeding at Cape Crozier.

Adélie Penguin (*Pygoscelis adeliae*).—The Cape Crozier Adélie Penguin population is among the largest known for this species. An estimate derived from analysis of aerial photographs taken in 1966 placed the breeding population at about 102,500 pairs, 13,500 of which nested in a rookery about 500 m east of the main rookery and separated from it by an ice field and cliffs (Butler and Müller-Schwarze 1977). There are about 166,000 non-breeding birds that also spend time in the rookery each season, mostly during very brief visits in December (Ainley, unpubl. data).

Counts of adults, made in 2 of the few hundred breeding colonies at Crozier during 4 seasons, were continued to late January in 1974–75 (Fig. 2). On 16 October 1962, our earliest date at Crozier, no Adélies were present in the pack ice immediately offshore or in the main rookery. We saw the first in the pack ice on 22 October and in the rookery on 23 October. On our next earliest arrival at Crozier, 19 October 1969, about 200 Adélies were present at the rookery. Most were standing or lying on snow slopes or on the beach, and none appeared in the 2 census colonies until 21 October. During 1968, 1971, and 1975 the maximum number of adult penguins in the rookery was attained by 11 November. In 1969 the maximum occurred on 6 November, an early date presumably related to light pack ice conditions (Ainley and LeResche 1973). Arrival at the breeding grounds thus occurred later at Crozier than at more northern Signy Island where peak numbers occurred on 4 November in 1950 (Sladen 1953) but slightly earlier than at nearby Cape Royds (100 km from Crozier) where peak populations occurred 11 to 15 November in 4 seasons (Taylor 1962, Stonehouse 1963, Yeates 1968). A second but lower peak, composed largely of one member of each pair guarding chicks, failed breeders, and young non-breeders, occurred in late December (31 December in 1974).

In 1968 and 1969 the mean date of clutch completion ranged from 16 to 20
November (Ainley and LeResche 1973). First eggs were found on 3 November in 1967, 1968, 1974, and 1975, and on 5 November in 1969. The last eggs were laid during the first week of December but young rarely fledged from them. The first fledglings departed the rookery in late January (29 January 1970; none had departed by 27 January 1975). All chicks and most adults were gone 2 weeks later. A few hundred adults came ashore in late January to begin molt and must still have been there well past the date when the last breeders departed.

Chinstrap Penguin (*Pygoscelis antarctica*).—Nine individuals, most of which were captured and banded (see Sladen et al. 1968), were seen on 15
occasions during 4 years. These records were as follows: 1963—1 bird on 24 February (T. Taylor); 1964—1 bird which began molt on the 27th, present 22 to 27 February (W. Emison); 1965—1 bird on 2 February (D. Thompson) and 2 birds on 17 February, present 15 January to 21 February (W. Sladen and others); 2 birds, 1 of which began molt by the 13th and the other of which began molt on the 20th, present 13 to 21 February (W. Emison); and 1 bird present and molting 20 to 21 February (R. Wood and W. Emison). All but 1 were seen only at the beach and evidently all had come ashore to molt. Since many of the last-dates-seen for these birds were the dates we left Crozier, many of these birds remained much longer than the spread of dates indicate. Because no persons were at Cape Crozier beyond mid-February after the 1965-66 season, Chinstraps, usually seen in late February, were not observed in later years. Watson et al. (1971) include the 1962-64 records in their summary and list only one other record for the entire Ross Sea. Since Chinstraps have begun to breed in recent years on the Balleny Islands (Sladen 1964), several hundred kilometers west of the Ross Sea, one might expect an increase in their visits to the Ross Sea.

Southern Giant Fulmar (*Macronectes giganteus*).—The giant fulmar is another non-breeding member of the Crozier avifauna. Two banded birds captured (run down when winds were calm) originated from Macquarie Island, about 1000 km to the northwest, the closest known nesting colony (see Wood et al. 1967). We recorded this species in all years except 1974-75 on 27 dates between 4 January and 14 February. We have no explanation for their absence during that one season; if they arrived after our departure on 27 January, they were unusually late (Table 1). Several birds were usually present on any day. The average counted per day was 7 to 15 birds ($\bar{x} = 8.5$, n = 50 groups, SD = 12.9) although 83 were present on 17 January 1967, a year when they seemed more abundant than usual (average count for dates that year: 25.6, SD = 26.6, range = 9 to 83). The ratio of light to dark phase birds was 1:6.4 for counts made on 22 days in 6 seasons (n = 233 birds), a ratio similar to that observed by Wilson (1907) in waters of the Pacific Ocean south of the Antarctic Convergence. Giant fulmars, which were never observed feeding in the penguin rookery, were observed feeding on penguin carcasses left floating in the water by leopard seals (*Hydrurga leptonyx*); they were often harassed by skuas interested in the same carcasses. Giant fulmars often roosted on icebergs and on snow slopes at the sea edge.

Southern Fulmar (*Fulmarus glacialisoides*).—Southern Fulmars were recorded during only 3 of the 12 years. The first record was of a bird seen on 19 December 1967 (Sladen et al. 1968); another was recorded on 19
December 1969, and individuals were seen 2 or 3 times during the following week, and 1 was observed on 17 December 1970. All were seen as they flew along the beach. This species was not included among records for the southwestern Ross Sea reviewed by Watson et al. (1971). Owing to this local paucity of records, Spellerberg’s (1971) comment that they were “often seen” during March 1964 at the mouth of McMurdo Sound, about 110 km west of Crozier, is very interesting. The nearest breeding locality is at the Balleny Islands (Watson et al. 1971).

**Antarctic Petrel (Thalassoica antarctica).**—Antarctic Petrels, recorded in all years except 1963, 1964, and 1966, were seen 21 times on 13 dates between 23 November and 1 January. Sixteen of the observations and 19 of the dates fall between 2 and 23 December. Observations discussed by Spellerberg (1971) indicate that they remain in the southern Ross Sea through February. They rarely occurred as solitary individuals, as also noted by others (e.g. Darby 1970); the largest flocks contained 30 birds on 1 January 1970, 40 on 26 December 1962, and 45 on 23 December 1974. Only 9 of the 21 observations were of single birds. The mean number of birds per sighting was 8.8 (n = 21, SD = 13.3). Often the flocks flew 50 to 100 m above the sea, and on several occasions they meandered high above the Adélie Penguin rookery.

For 12 of 14 visits from 1967 to 1975 when wind velocity was recorded, Antarctic Petrels were present only during southerly winds of 50 km/h or greater. Under these conditions, the petrels would have had to fly up wind to reach Cape Crozier from the sea (see further discussion under Snow Petrel). Their nearest breeding colony is King Edward VII Peninsula several hundred kilometers to the east (Watson et al. 1971).

**Snow Petrel (Pagodroma nivea).**—Snow Petrels were seen almost daily from late November until late December, but after the first week of January they were seen only 7 times. We recorded them on 49 dates but no doubt they were present on more. The earliest sighting, occurring in 2 different years, was 11 November (Table 1) and the latest was 21 February. Siple and Lindsay (1937) recorded 13 March (1934) as the latest date in the southern Ross Sea. The closest known breeding localities are Cape Hallett and King Edward VII Peninsula (see Watson et al. 1971).

Snow Petrels usually occurred singly or in small, loose flocks. During 1974 the mean number of petrels per sighting was 2.0 (131 sightings, range 1 to 13 birds); single birds were seen on 83 of those occasions. Rarely were they present in large flocks: 17 in one flock on 11 December 1964, 19 on 27 November 1975, 22 on 3 December 1964, and 31 on 24 December 1963. Many times they flew well inland and on several occasions they investigated
the cliffs and talus slopes of Post Office Hill 3 km inland. Twice in 1974 and once in 1975 we saw 3 to 5 individuals flying inland together at an altitude that must have exceeded 600 m.

Analysis of the 1974–75 records revealed that Snow Petrel occurrence at Cape Crozier was related to wind speed and direction and to the extent of pack ice cover. They occurred daily from 11 November to 25 December and the number seen per hour of observation was related directly to the strength of southerly (offshore) winds ($r = 0.68$, $SD = 2.9$, $t = 4.36$, $P < 0.05$). No counts were made during winds higher than 96 km/h that year but, based on observations from the hut window during stronger winds in other years, they appeared to be abundant when wind velocity exceeded that speed. On 27 November 1975, we ventured from the hut when winds were blowing 112–120 km/h with higher gusts. During an hour of observation we counted 68, a figure that fits with the correlation just discussed. They were definitely making headway into the winds, seemingly rather easily. There was no relationship in the 1974–75 data between the number seen and the strength of northerly (onshore) winds ($r = 0.17$, $SD = 0.8$, $t = 0.70$, $P > 0.05$).

The mean number seen per hour of observation during winds that were calm, northerly (onshore), southerly (offshore) but 33 km/h or less, and southerly but greater than 33 km/h, respectively, was 0.02, 0.79, 0.38, and 4.2 petrels per hour. Using a one-way analysis of variance (Steel and Torrie 1960:113) we find these 4 means to be dissimilar ($F = 5.51$, $df = 3$ and 41, $P < 0.05$); but computing the analysis without the value for southerly winds greater than 33 km/h (4.2) gives a set of similar means ($F = 1.36$, $df = 2$ and 21, $P > 0.05$). Hence larger numbers of Snow Petrels at Crozier occurred only when southerly, offshore winds exceeded 33 km/h; as the winds increased so did their numbers. The petrels occurred at about the same rate under all other wind conditions.

The number seen at Cape Crozier was also affected by the pack ice cover. Generally speaking, Snow Petrels were rarely seen earlier than mid-November; before then the pack ice was normally heavy and often covered the sea completely. They were also rare after 1 January when there was usually no pack ice present. During the intervening period when Snow Petrels were present almost daily, the number seen per hour was related inversely to the percentage of the sea covered by ice ($r = 0.442$, $SD = 29.99$, $t = 2.95$, $P < 0.05$). Confusing the issue somewhat, however, was the fact that during that same period the percentage of ice cover was related inversely to the strength of the wind ($r = 0.6365$, $SD = 24.60$, $t = 5.06$, $P < 0.05$). Strong southerly winds, which also attracted petrels, blew the pack ice offshore decreasing the percentage of ice cover; light winds had little effect and northerly winds, which never exceeded 38 km/h, concentrated the pack against the shore. Since we rarely
observed Snow Petrels feeding in the open water (taking advantage of the conditions wrought by strong southerlies), it is difficult to surmise the reason for their marked response to wind and ice conditions. Wilson (1907) noted Snow Petrels feeding on euphausiid crustaceans and occasionally fish, thrown by breaking surf onto the edges of ice floes. The petrels seen at Crozier during strong winds might have been seeking such an opportunity, but under those conditions the pack ice edge was usually pushed too far for us to observe. On a windy day in December 1975, when the ice edge met the land at Crozier, we observed petrels flying along the edge: we were able to view them with 8X binoculars at a distance of 1 km. but none appeared to be feeding.

Snow Petrels tended to fly along pressure ridges in the pack ice and, when ice was sparse, flew back and forth for several minutes from one floe or berg to another. In so doing they were perhaps seeking and taking advantage of updrafts created by the ice, but may have been searching for under-ice organisms available only along exposed edges of ice. We seldom saw Snow Petrels alight. One bird apparently stopped to rest for a few hours on an ice floe (winds were light); another alighted on the edge of the beach ice to investigate a penguin head remaining from a leopard seal kill. On 2 other days (brash ice present, winds calm) they were observed in what was possibly feeding activity; they repeatedly dropped to the water for an instant and, keeping the wings fully extended above the back, pecked at (objects in ?) the water.

**Wilson’s Storm-Petrel** (*Oceanites oceanicus*).—Wilson’s Storm-Petrels were seen in all years except 1967 and were recorded 21 times on 18 different dates between 4 December and 8 February. A single bird seen by Hallett (1973) on 6 January 1971, is included in the tally. Twelve of the observations and 10 of the dates were between 4 and 23 December, indicating a peak in occurrence during that period. Observations reviewed by Spellerberg (1971) suggest they depart by late February. Only single individuals were present except once when 2 birds were seen flying together: most were observed as they flew along the beach, but 9 times they flew well inland. Twice single birds fluttered about the talus slope of Post Office Hill, seemingly suitable nesting habitat, but they never alighted. Watson et al. (1971) overlooked the occurrence of the species in the southwestern Ross Sea, but both Wilson (1907) and Spellerberg (1971) reported them there. The nearest known breeding site is Cape Hallett, several hundred kilometers to the northwest (Watson et al. 1971).

**Brown Skua** (*Catharacta lonnbergi*).—Five Brown Skuas have been seen at Cape Crozier. These were identified on the basis of size (see Parmelee et al. 1977:fig. 4), color and voice. Those individuals present on 6 November
1966 (collected: a female, USNM 533558), 12 December 1967, 19 December 1969, and 29 November 1970 have been reported previously (Wood et al. 1967, Sladen et al. 1968, Schlatter and Sladen 1971). The first Crozier record of a single bird present on 9 and 10 January 1964 has not been reported. All Brown Skuas were observed on or very near the beach, usually within clubs (R. P. Schlatter, pers. comm.) of South Polar Skuas. This species has been noted only once previously in the southern Ross Sea (see Watson et al. 1971). The species is suspected to breed on the Balleny Islands, but otherwise the closest known breeding site is Macquarie Island (Watson et al. 1971).

South Polar Skua (Catharacta maccormicki).—The South Polar Skua population at Cape Crozier consists of 1900 to 2000 breeding birds and an estimated 200 to 400 non-breeders (Wood 1971). Breeding birds nested in 6 discrete areas. The biology and dynamics of breeders in this population were described by Wood (1971); similar information on non-breeders was presented by R. P. Schlatter (pers. comm.).

In mid-to-late October only 1 or 2 were seen on any day, usually near the beach or over the pack ice. The earliest skua was seen on 19 October in 1962 and 1969. During 1975, nesting area occupation by skuas was observed by censusing birds each morning (ca. 09:00) in a \(20 \times 100\) m plot at the site of the old hut and helicopter landing pad. That season the first skua on the ground was seen on 27 October (the previous season it had been 23 October). They occurred in the study area sporadically for the following week, although increasing numbers were seen flying about near the beach or over the sea. Thereafter the number of territorial skuas increased steadily (Fig. 3). The most spectacular increase in numbers occurred between 7 and 13 November 1975, coincident to the period when Adélie Penguin numbers increased most sharply. A very fierce storm, and consequently an ice-free sea, occurred then too. The sharp increase in penguin numbers was a direct result of the storm and sea conditions (see Ainley and LeResche 1973), but whether skua arrival was also directly related is not known. The maximum number of occupied territories was reached about 21 November and numbers declined in the following week. The peak and decline may have represented birds attempting unsuccessfully to establish new territories in the area. Egg laying began on 25 November when the number of territories leveled off. The earliest and latest known egg laying dates at Crozier are 17 November and 31 December, respectively.

The latest we remained at Cape Crozier was 2 March (1963). Our observations suggest that most skua young probably fledge by late March or early April. Most adults probably depart by then, too; this schedule is supported by the records reviewed in Spellerberg (1971).
Fig. 3. Census results showing number of adult skuas, number of occupied territories, and number of eggs laid each day for an area near the old hut site at Cape Crozier, 1975-76 season.
Southern Black-backed Gull (*Larus dominicanus*).—An adult Southern Black-backed Gull was seen by R. T. Peterson and Sladen on 15 and 16 November 1965. Another, a second year individual, was present from 24 November until 3 December 1969. It fed with the skuas on remains of Adélie Penguins left by leopard seals. This species had been noted only once before in the Ross Sea (see Watson et al. 1971). The closest breeding locality is Macquarie Island.

**DISCUSSION**

A continuous belt of pack ice surrounds Antarctica. Vertebrates best adapted for life in that zone should be those found in its interior reaches where the ice is most persistent. The observations from Cape Crozier, deep within the pack ice of the southern Ross Sea, help us to characterize the avian community in that environment. Primary species in the community, in terms of regularity of occurrence and relative abundance, are the Adélie Penguin, Emperor Penguin, Snow Petrel, South Polar Skua, Southern Giant Fulmar, and Antarctic Petrel. Secondary species are Wilson’s Storm-Petrel, Chinstrap Penguin, Southern Fulmar, Brown Skua, and Southern Black-backed Gull. The order of listing might well be different had observations been made farther offshore. Particularly interesting in light of the reports by other researchers (see below) is the rare presence of Chinstrap Penguins, Brown Skuas, and Southern Black-backed Gulls, the relative rarity of Southern Fulmars, and the absence of Cape Pigeons (*Daption capense*), prions (*Pachyptila* spp.), and Arctic Terns (*Sterna paradisaea*).

Murphy (1936:593) considered the Southern Fulmar to be second only to the Snow Petrel for its ubiquity in the pack ice. That is probably true, however, only for the periphery of the pack ice zone where the ice is loosely concentrated and where most observations, including Murphy’s have been made. Deep within the pack ice of both the southern Ross and Weddell seas fulmars have proved to be quite rare (Cline et al. 1969, Watson et al. 1971, Halle 1973, this study). Cape Pigeons, though not yet observed at Crozier, have been reported in the southern Ross Sea twice: single birds seen by Halle (1973) at 72°S off Cape Hallett in 1971 and by Wilson (*in* Lowe and Kinnear 1930) at 76°54’S in 1912. On the other hand, Spellerberg (1971) mentioned in passing (!) that for waters “off the northern tip of Ross Island” during early March 1964 “the Cape Pigeon . . . was by far the commonest bird sighted.” Many other observers have said the same for Antarctic Petrels, a species quite similar in coloration and size (see Darby 1970), in those waters at that time of year. In view of their scarcity in the region in our and others’ experience, their superficial similarity to another abundant species,
and the extreme characteristic of Spellerberg's records, one must view the latter with suspicion. Finally, no records exist for the Arctic Tern or for prions at Crozier. Arctic Terns have never been reported in the Ross Sea, although Cline et al. (1969) reported them at least as far as 74°37'S in the Weddell Sea; prions have been seen as far south as 73°38'S in the Ross Sea by Darby (1970) and to 69°36'S in the Weddell Sea by Cline et al. (1969).

The Crozier-area avifauna reached its greatest complexity in terms of population sizes, frequencies of occurrence, and variety of species during December and, to some extent, January (Table 3, Fig. 4). One factor determining that pattern may have been the timing of the plankton bloom which also affects the timing of breeding (see Beck 1970). Balech et al. (1963) found that phytoplankton in the Pacific sector of Antarctica reached peak volume during December and then declined slowly through May (Fig. 4): zooplankton, which feeds upon the phytoplankton and upon which the birds largely feed, should lag slightly behind the phytoplankton in their abundance cycle. The peak in bird occurrence, avian community complexity, and plankton biomass thus corresponded quite closely and were probably related. Why birds did not remain abundant throughout the December to May period of high plankton abundance is discussed below.

An equally, if not more, important factor affecting the birds seemed to be the pack ice conditions. In the Weddell Sea, Cline et al. (1969) found highest concentrations of most avian species where ice was light (10 to 30% cover) to medium (40 to 60%). Few species preferred the extremes of open water and total ice cover. Their observations fit with those averaged over a 5-year period at Crozier where the pack ice began to disappear in late October and was completely gone by January (Fig. 4). The ice cover declined most rapidly during December, from 60 to 10%, precisely the range when the largest number of species and the highest populations occurred. Only the Chinstrap Penguin and giant fulmar arrived after the pack ice disappeared entirely. Even so, Cline et al. (1969) found Chinstrips in the Weddell Sea only where pack ice was light, and giant fulmars mainly where ice was light or absent. The disappearance of the pack ice also corresponded to the disappearance of a Crozier breeding species, the Emperor Penguin, which, after fledging of young in December, requires ice on which to molt. Much earlier in the summer, the presence of 2 other Crozier breeding species (Adélie Penguin and South Polar Skua) also was affected by change in the pack ice: their arrival corresponded to the period when the pack ice first began to lessen. Some open water is beneficial during breeding because it increases the accessibility of food (see Ainley and LeResche 1973) but, when breeding is completed, Adélies, like other Antarctic penguins, are better able to molt in heavy pack ice (Cline et al. 1969).
### Table 3

**The Average Number of Birds Recorded Per Date During “Weekly” Periods**

<table>
<thead>
<tr>
<th>Weekly Period</th>
<th>Chinstrap Penguin</th>
<th>Southern Giant Petrel</th>
<th>Southern Fulmar</th>
<th>Antarctic Petrel</th>
<th>Snow Petrel</th>
<th>Wilson's Storm-Petrel</th>
<th>Brown Skua</th>
<th>Southern Black-billed Gull</th>
<th>Total Species</th>
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<td>Oct</td>
<td></td>
<td></td>
<td></td>
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<td>Dec</td>
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<td>3 (5)</td>
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1 Weekly periods (1, 2, & 4) were extended to 8 days to produce 4 periods per month.

2 Breeding species are included in parentheses only in extreme right column.

Although some open water must be available for Antarctic birds to feed, it seems strange that they apparently preferred water partly covered with ice floes. Except for short term requirements for molting in the penguins and the breeding requirements of the highly specialized and remarkably adapted Emperor Penguin, Antarctic birds should not need ice for resting. They do indeed use it for that purpose but, since their relatives elsewhere do not enjoy the luxury of floating ice islands, it should not be a factor critical to survival in the Antarctic. Possibly the diversity of environment offered by the pack ice is the important factor. Based on what little we know about the feeding...
ecology of these birds, they are conspicuously opportunistic in both feeding behavior and diet. With the exception of the penguins, all scavenge on surface prey or carrion. Light to medium ice cover perhaps provides these birds with several opportunities for feeding not available in open water or heavy ice:
they can feed on open water organisms, ice edge organisms, and under-ice organisms. As Cline et al. (1969) pointed out, they can feed on the many organisms often crushed between rapidly moving floes and, as discussed earlier, can find potential prey thrown up and stranded by wave action upon floes. Thus within light to medium pack ice more kinds of opportunities for food seem available, and this might even relate to our earlier discussions about why winds “attract” birds to Crozier. Wind can rapidly change the configuration and density of pack ice, especially where the ice is relatively loose, and in so doing might rapidly present some of the above opportunities. It would seem worthwhile to observe the avian pack ice community of Antarctica with this idea of habitat complexity and diversity of opportunity in mind.

SUMMARY

Observations of the birds at Cape Crozier, Ross Island, within the southernmost reaches of the Ross Sea in Antarctica were summarized for 12 summers during the period 1961–76. Data on the occurrence of 11 species were presented. The Emperor Penguin breeding colony at Crozier declined in size due to an unfavorable nesting situation and perhaps unknown factors. Wind conditions affected the occurrence of Snow Petrels and Antarctic Petrels; winds under 38 km/h had little effect but offshore winds above 38 km/h attracted significant numbers to the area. Rather interesting were records for Chinstrap Penguins, Brown Skuas, and Southern Black-backed Gulls, the relative rarity of Southern Fulmars, and the absence of Cape Pigeons, prions and Arctic Terns.

The avifauna was most diverse in terms of population sizes and variety of birds during December, the month of peak plankton concentrations and of changing ice cover on the sea. The birds may have responded particularly to the latter because such conditions offer the greatest diversity of habitat and foraging opportunity.

ACKNOWLEDGMENTS

The research at Cape Crozier was part of the United States Antarctic Research Program funded by grants to W. J. L. Sladen and D. G. Ainley from the National Science Foundation, Division of Polar Programs. We wish to thank G. A. Llano, Biology Program Director in the latter office, who offered much guidance and assistance throughout the whole tenure of our work. We wish also to thank the persons from the United States Antarctic Research Program and the U.S. Navy, Operation Deepfreeze, for their assistance in logistics. We are extremely grateful to the many persons who spent time with us at Crozier for their comradeship and for the observations they contributed, and to G. E. Watson for helpful comments on the manuscript. This is Contribution No. 105 of the Point Reyes Bird Observatory.

LITERATURE CITED


POINT REYES BIRD OBSERVATORY, 4990 STATE ROUTE 1, STINSON BEACH, CA 94970 AND DEPT. OF PATHOBIOLOGY, 615 N. WOLFE STREET, BALTIMORE, MD 21205 (RCW and WJLS): present address of RCW: RT. 1, 3921 MILLER ROAD, KINGSVILLE, MD 21087. ACCEPTED 31 OCT. 1977.
FOOD SIZE, FOOD TYPE, AND FORAGING SITES OF RED-WINGED BLACKBIRDS

STEPHEN W. WILSON

Before the onset of the breeding season, Red-winged Blackbirds (Agelaius phoeniceus) shift from an herbivorous to an insectivorous diet (Hintz and Dyer 1970). Morton (1973) suggested that such seasonal changes in feeding are important in providing a high protein diet for rapidly growing nestlings. During the time nestlings are being fed, both quality and quantity of food are critical for rapid growth.

Feeding efficiency, the maximizing of the number of calories delivered to the nestlings per unit time, is important because the parent birds are limited in the number of feeding trips they can make per day. One method of increasing feeding efficiency may be selection of the largest food items relative to the time and energy expense of capture. Smaller insects are ordinarily more abundant than larger insects and either obligate selection of only large insects or random selection of all insects might be energetically inefficient. Nevertheless, one might expect a shift to the larger size spectrum with the sizes selected a function of energy expended in search and capture (Emlen 1966). In this regard, Hespenheide (1966) noted that some species of birds do choose the largest food items in relation to energy expended. Wilson (1975) noted that, within specified limits, success of prey capture increases with an increase in prey size. Feeding efficiency might also be increased by selection of specific food types such as slow-moving insect nymphs and larvae.

Another method of increasing feeding efficiency may be by reduction of competition, especially intraspecific competition. If different segments of the population, for example different age classes or sexes, foraged in a dissimilar manner or in different locations, competition might decrease, leading to an increase in foraging efficiency. Many authors (e.g., Selander 1966) have shown that males and females in many sexually dimorphic species forage at different sites on essentially different prey populations.

The purpose of this study was to evaluate the importance of food size, food type, and foraging sites in relation to the feeding efficiency of Red-winged Blackbirds while feeding nestlings. The study consisted of determining: (1) the size of food items fed nestlings versus the sizes potentially available, (2) the developmental stage of the food eaten, and (3) the importance of intraspecific competition for food during the breeding season.
MATERIALS AND METHODS

Red-wings were studied at a marsh (ca 3 ha) and adjacent field (ca 3 ha) on the north shore of Lake Springfield, 3.2 km south of Springfield, Missouri. Dominant vegetation in the marsh consisted of cattails (*Typha latifolia*), water willow (*Justicia americana*), bulrush (*Scirpus lineatus*), arrowhead (*Sagittaria latifolia*), cutgrass (*Leersia* sp.), and black willow (*Salix nigra*). Grasses were dominant on the field which, during the summer, was mowed bi-weekly.

I collected food samples from 3-to-8-day old nestlings, using Orians’ (1966) pipe-cleaner, neckcollar technique, between 08:00 and 11:00 (CDT) on alternate days from 27 May to 5 June and from 20 June to 4 July 1974. This time period was chosen to keep the data consistent and to prevent starving the nestlings, thus adding a possible bias. Each food sample represented 11/2 to 2 h of food delivery. Thirty samples representing ca 53 h of feeding time were collected. Food items were identified to family (when possible) and length measured to the nearest 0.5 mm.

Sweepnet samples were taken at 5 stations, 3 on the field and 2 on the marsh, every 2 to 3 days between 08:00 and 11:00 from 27 May to 8 July 1974. Each sample was composed of 10 sweeps with a heavy-duty sweepnet scraping the ground and vegetation just above the ground. The purpose of the sweepnet samples was to obtain an index to the size distribution of organisms a bird might encounter if feeding were random within these habitats. It is unlikely that an individual bird would encounter this full range of sizes at all times and in all places. Nevertheless, the sweep samples serve as a measure of potentially available prey size distribution. Janzen (1973) felt that the composition of insects collected by sweep sampling and actually present in the foliage was in general agreement.

Foraging activity data were gathered on the field because dense vegetation prevented similar observations on the marsh. Birds foraging on the field were observed for a 90 min period between 08:00 and 11:00 every 2 to 3 days from 27 May to 9 July 1974 for a total of 30 h. Any bird exhibiting feeding behavior, either on or within ca 1.5 m of the ground, was counted as feeding. The number of male and female Red-winged Blackbirds on the field was recorded at 10 min intervals for the 90 min period in the manner of Austin and Smith (1972).

RESULTS

Comparison of the number of male and female Red-winged Blackbirds foraging on the field with the number expected (if male and female population sizes were equal) by the G-test (Sokal and Rohlf 1969) indicated a significantly higher use of the field by males than by females ($P < 0.005$; Table 1). The males that foraged on the field consisted of breeding and possibly a few non-breeding individuals. Two population censuses were made along the periphery of the marsh: 14 males and 14 females were counted on 20 June and 13 males, 13 females were counted on 18 July 1974. As males were more conspicuous than females (e.g., calling on their territories), the number of females was probably underestimated. Furthermore, females generally outnumber males in Red-winged Blackbird breeding populations, which strengthens the conclusion that males are selecting the field on which
Table 1

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<tr>
<th>Date</th>
<th>Number* of</th>
<th>Ratio of females/males</th>
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<tbody>
<tr>
<td></td>
<td>males</td>
<td>females</td>
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<tr>
<td>May 27</td>
<td>20</td>
<td>5</td>
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<tr>
<td>28</td>
<td>19</td>
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<td>June 1</td>
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<td>July 2</td>
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<tr>
<td>4</td>
<td>71</td>
<td>3</td>
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<tr>
<td>9</td>
<td>54</td>
<td>1</td>
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<tr>
<td>Total</td>
<td>523</td>
<td>39</td>
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</table>

* Sum of the number of males and females observed in each 10 min time period for the 90 min observation period.

To forage (Haigh 1968, Dolbeer 1976). In any event, in order for these data (Table 1) to be a simple reflection of an unbalanced sex ratio, the population would have to consist of at least 91% males ($P > 0.05$) for even if the population consisted of 90% males, which is unlikely, there would still be a significant difference between observed and expected male/female activity on the field ($P < 0.01$).

Because males and females appeared to forage in different locations, the sizes of potential prey organisms in 2 probable foraging areas, the field and marsh, were compared. Mann-Whitney U-test analysis indicated that the average size of organisms I caught on the marsh was significantly larger than the average size of organisms caught on the field (Table 2). Furthermore, 2-way analysis of variance revealed that the mean body length of representatives of 8 orders of arthropods on the marsh were larger than those on the field ($P < 0.001$), that the average length of representatives of the orders differed significantly ($P < 0.001$), and that there was no significant interaction between location and taxa ($P > 0.10$; Table 2). Because sample sizes were unequal, randomly selected subsamples of equal size were taken...
for each of the categories (i.e. 21 samples from the Collembola captured on the field, where $N = 227$; 21 samples from Orthoptera captured on the field, where $N = 32$, etc.). These data were transformed to their common logarithms and then analyzed.

Comparison of the size frequency of potentially available prey organisms with nestling food samples by the Mann-Whitney U-test showed that nestlings were fed significantly larger items ($P < 0.001$) than were potentially available (Fig. 1). Because potential prey organisms in the marsh were significantly larger than those in the field and in order to test whether the size frequency difference between nestling food and sweepnet samples was due to sampling location, I compared the size frequency distributions of marsh organisms and nestling food samples (Fig. 1). Mann-Whitney U-test analysis revealed that nestling food organisms were significantly larger than potential prey from the marsh ($P < 0.001$).

In order to evaluate the type of prey in terms of insect developmental stage fed to nestlings, I compared the sizes and frequency of occurrence of adult, nymphal, and larval insects captured in the marsh and fed to nestlings. All non-insect arthropods appeared to be adults and, for purposes of analysis, were counted as such.

Mean body lengths of organisms captured by sweepnet sampling in the marsh and taken from nestlings for each of 3 insect developmental stages (adults, nymphs, and larvae) are compared in Table 3. Two-way analysis of variance of these randomly selected, equal-sample-sized, log-transformed data (see above) indicated: (1) a significant difference in size between what was

<table>
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<th>Order</th>
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<th>Mean ± SE (mm)</th>
<th>N</th>
<th>Mean ± SE (mm)</th>
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<td>Collembola</td>
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<td>0.60 ±0.171</td>
<td>39</td>
<td>0.76 ±0.254</td>
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<td>5.09 ±0.297</td>
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<td>7.97 ±0.328</td>
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<td>3.90 ±0.33</td>
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<td>639</td>
<td>3.00 ±0.30</td>
<td>345</td>
<td>3.70 ±0.41</td>
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<tr>
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<td>130</td>
<td>3.40 ±0.39</td>
<td>135</td>
<td>4.90 ±0.42</td>
</tr>
<tr>
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<td>2.63 ±0.255</td>
<td>654</td>
<td>3.16 ±0.239</td>
</tr>
<tr>
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<td>108</td>
<td>2.11 ±0.263</td>
<td>39</td>
<td>3.30 ±0.34</td>
</tr>
<tr>
<td>Araneae</td>
<td>63</td>
<td>2.28 ±0.36</td>
<td>73</td>
<td>3.00 ±0.43</td>
</tr>
<tr>
<td>All Organisms*</td>
<td>2063</td>
<td>2.76 ±0.139</td>
<td>1685</td>
<td>4.79 ±0.188</td>
</tr>
</tbody>
</table>

* Includes arthropods and other organisms.
Fig. 1. Percent of body lengths of sweepnet samples and nestling food samples. A. Combined marsh and field sweepnet samples, $N = 3768$. B. Nestling food samples, $N = 112$. C. Marsh sweepnet samples, $N = 1685$. $\bar{x} = \text{mean} \pm \text{standard error.}$
fed nestlings and what prey organisms were potentially available \((P < 0.005)\), (2) no significant difference among the sizes of developmental stages \((P > 0.5)\), and (3) a significant interaction among developmental stages within the sweepnet samples and nestling food samples \((P < 0.05)\).

If the nestlings are fed items selected at random, the percentage of adults, nymphs, and larvae fed to the nestlings should correspond to the percentage of adults, nymphs, and larvae occurring in the feeding area (Fig. 2). However, a G-test of arcsine-transformed data indicated that there was a signifi-
cantly higher proportion of nymphs and larvae in the nestlings' diets than in the marsh sweepnet samples ($P < 0.005$).

**DISCUSSION**

The observation that male Red-winged Blackbirds used the field as a foraging site significantly more often than females suggests a sexual difference in foraging site preference. Selander (1966) noted that male and female Red-winged Blackbirds have been observed feeding in sexually segregated flocks in the fall, but to my knowledge this has never been observed during the breeding season. After 216 h of observation during the breeding season, Brenner (1968) noted that females were never seen feeding off the marsh. I observed few females feeding on the field (Table 1), but many feeding in the marsh.

The importance of sexual differences in foraging sites can be related to the role of the female in feeding nestlings. Verner and Willson (1969) indicated that males do not generally feed nestlings. If a strict time-energy budget exists for the female in feeding nestlings, then any mechanism that may reduce competition for food would be advantageous. Even a slight segregation of foraging sites at a critical time (such as during nestling feeding) may reduce intraspecific competition for food.

In addition to the observation that females fed significantly less often in the field than did males, and that one probable female feeding area was the marsh, I noted that these locations offer significantly different-sized prey organisms. Comparison of the arthropod faunas of the marsh and field indicated that the average size of organisms occurring in the marsh was larger than that of those on the field. Hence, the marsh was likely a more "profitable" place to forage in terms of the number of calories per organism than the field.

That prey items fed to nestlings differed significantly in size from what was potentially available can also be related to the role of the female in feeding nestlings. During the first 9 days of life, nestling weight increases ca 700% (Robertson 1973). Using the existence-energy equations of Ken-deigh (1970) and Wiens and Innis (1971), a 43.5 g female Red-winged Blackbird (an average of 10 specimens from the University of Oklahoma collection) would require ca 32.6 kcal day$^{-1}$ and a nestling would require ca 147 kcal during the first 9 days after hatching (nestling weight data from Robertson 1973). These results are similar to those found by Brenner (1968) and Haigh (1968). The average size of items fed to nestlings in my study was 13.2 mm (Fig. 1). Orians (1973) estimated that a 13 mm orthopteran contains about 50 cal. Thus, accepting these assumptions, during the first
9 days, a parent bird would have to deliver ca 2940 “average-sized” items per nestling. This tends to support the contention that a strict time-energy budget exists for the female while feeding nestlings.

From an energy standpoint, it would be advantageous to ignore smaller and/or fast-moving food items and to feed on larger and/or slower moving food items (i.e. dragonfly tenerals, insect larvae, etc.). Comparison of the frequency size distributions of the prey fed to nestlings and the prey potentially available to nestlings (Fig. 1) supports the contention that small prey items are ignored. Both distributions seem to reflect log-normal distributions as found by Schoener and Janzen (1963), but with a shift to larger sizes in the nestling prey distribution.

The apparent selection for larvae and nymphs might be attributed to their soft anatomy, their ease of capture, or both. Pulliam (1975) postulated that animals may show partial preferences in feeding when nutrient constraints exist. Also, rapid assimilation of nutrients would favor rapid growth, and selection for softer food items could be an evolutionary response to the necessity for rapid food breakdown. Furthermore, a larva, nymph, or an emerging adult is easier to capture than a flying adult. Nevertheless, some hard insect parts are necessary for the mechanical breakdown of food (Bird and Smith 1961). West (1973) noted similar feeding patterns in Tree Sparrows (Spizella arborea). Alcock (1973) indicated that Red-winged Blackbirds have the ability to distinguish food items on the basis of visual and locational cues.

Two mechanisms, a tendency for males to feed in an area little used by females and a tendency for females to feed nestlings relatively large and soft food items, may be related to the role of the female in feeding nestlings and to the females’ strict time-energy budget as a result of having to feed rapidly growing nestlings unassisted. A female has the capability of making only so many feeding trips per day. If the number of trips per day is roughly constant, then the more calories of food brought to the nestlings per trip, the higher the probability that the young will be adequately nourished throughout the nestling period. A female could satisfy this food demand by bringing many small prey items per trip instead of a few larger items. However, it is unlikely that many small items can be gathered with less expenditure of time and energy than the same biomass represented by one or several larger, slower moving items unless the small items were highly clumped and constantly available which is unlikely to occur very often. Bird and Smith (1964), Snelling (1968), Hintz and Dyer (1970), and Voigts (1973) indicate that Red-winged Blackbirds feed on a wide variety of prey, which supports the contention that generally the birds do not exclusively use small, highly clumped prey.
SUMMARY

Female Red-winged Blackbirds were found to feed less often on the field than were males; this may reduce intraspecific competition. The average size of organisms captured by sweepnet sampling in the marsh, the area in which females possibly fed, was significantly larger than on the field.

The size of organisms fed to nestlings was significantly larger than if food selection were random. There was also an apparent preference for soft-bodied items. As females feed nestlings unassisted by males, time-energy budget constraints make it necessary for females to maximize feeding efficiency. Preferences in food size, food type, and foraging locations may serve to do this.

ACKNOWLEDGMENTS

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LITERATURE CITED


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WINTER TERRITORIAL AND FORAGING BEHAVIOR OF RED-HEADED WOODPECKERS IN FLORIDA

DEBRA MOSKOVITS

Red-headed Woodpeckers (Melanerpes erythrocephalus) demonstrate conspicuous seasonal differences in foraging behavior, engaging primarily in flycatching in the spring and summer (Nauman 1960, MacRoberts 1970, Jackson 1976) and in storing acorns for winter consumption in the fall (Bent 1931, Kilham 1958a). Many migrate to suitable habitats for gathering acorns in the fall, and subsequently concentrate their winter activities in defending their stored mast (Kilham 1958a, Bock 1970, MacRoberts 1975). Kilham (1958a) describes these phenomena in Maryland, and MacRoberts (1975) briefly discusses the species' wintering behavior in Louisiana.

I recorded activities and daily time budgets of 26 Red-headed Woodpeckers wintering in Highlands County, Florida, and describe in this report some behavioral changes that emerged during the study period. In addition, I analyze the interactions of Red-headeds with their sympatric congener, the Red-bellied Woodpecker (Melanerpes carolinus). I close with a brief discussion of the ecological relationships of these species and a comparison of the Red-headed with its western relatives, the Lewis' Woodpecker (Melanerpes lewis) and Acorn Woodpecker (M. formicivorus).

STUDY AREAS AND METHODS

Study areas.—From 11 October 1975 to 2 January 1976 I observed 17 Red-headeds that had established territories in a 1.2 km² scruffy flatwoods area in Highlands Co., 11 km south of Lake Placid, Florida. The low vegetation in this study site consisted largely of fetterbush (Lyonia lucida) and saw palmetto (Serenoa repens). Scrub oak (Quercus inopina) was the dominant species in large sections of palmetto scrub; other sections also contained large numbers of turkey oak (Q. laevis). Chapman’s oaks (Q. chapmanii) and live oaks (Q. virginiana) were present, but less abundant. Most oaks were 1–1.5 m tall. The only other trees in the area were swamp bay (Persea palustris) and red bay (P. borbonia), about 2 m tall, and occasional 18–20 m slash pines (Pinus elliottii). A number of burned pine stubs remained from a 1968 fire. Dry ponds, covered with grass (Andropogon sp.) and St. John’s wort (Hypericum nudiflorum), were scattered throughout the scrub.

From 14 November 1975 to 2 January 1976, and from 14 February to 4 March 1977, I observed some additional Red-headeds in a recently burned, open scruffy-flatwoods section of the Archbold Biological Station, about 7.5 km S of the first site. The vegetation in this area was similar to the site described above, the main shrubs being live oak (1.5–2 m tall). Further description of this habitat, along with a summary of the resident avifauna, appears in Woolfenden (1969).

Observations on Red-bellied Woodpeckers were also made in these 2 scruffy-flatwoods,
and in 3 other pine-dominated habitats of the Archbold Station: slash pine-turkey oak, sand pine scrub, and low flatwoods (Woolfenden 1969). Red-headeds occupy most of these habitats during the spring and summer, but move away for the fall and winter.

Methods.—I followed Red-headeds in the 2 study areas for about 250 h and recorded 36 h of timed observations. Immature Red-headeds were individually identifiable by the emerging patterns of red on their heads. Adults were harder to distinguish, but also had characteristic markings (spots of black on their heads, black streaks on their white wing patches) visible at close range. After learning to recognize individuals, I followed them for intervals of 15–45 min. Observations were concentrated on 10 of the 26 individuals. They were mostly made during the fall and winter of 1975–76. I returned to the same areas for 1 week in May 1976, and again in February 1977 for observations on the birds’ activities during their last month in winter territories.

Each Red-bellied Woodpecker was followed for 10–15-min intervals, or until the bird was lost. I visited different sections of the study area each day, recording about 180 h of observation with this species (30 h of timed observations). Results of the Red-bellied study are reported here only as they relate to the ecology of the Red-headeds.

The woodpeckers’ activities were timed with a stop-watch, and divided into 3 main categories following Reller (1972): (1) foraging, when the birds were actually feeding or gathering mast; (2) maintenance, when they were engaged in resting, preening, or roost-hole excavating; and (3) territorial defense.

RESULTS

Dispersion in fall.—In late summer or early autumn, Red-headeds migrate to open areas containing abundant mast, where they establish individual territories (Kilham 1958a; pers. obs.). They will also remain on their breeding ground if they happen to nest by an open area or clearing where the mast crop is abundant the following fall (Bock 1970; pers. obs.). The latest records for Red-headeds on their summer territories in the denser pine-habitats of the Archbold Biological Station, from 1969–1977, range from 20–30 September (unpubl. records of Archbold Biological Station).

From 2–10 October, I followed 2 adult and 3 young Red-headeds that were foraging together in oak scrub on the primary study site. The juveniles occasionally foraged independently, but normally followed the adults, begging incessantly. However, rather than feeding the young, the adults chased them away, at times even pecking them. Only once did I see a Red-headed feed its young. In contrast, I saw Red-bellieds, which did not separate into individual territories, feed their young well into the first half of November.

Aggressive encounters between foraging Red-headeds were common during the early fall, with interactions between juveniles and adults being milder than those within the same age class. Interspecific squabbles also occurred at this period, especially at storage posts. Red-headeds had greater difficulty driving other species away during the early fall than they did later in the season, but throughout the study they dominated every interaction.

In early October, Red-headeds, Red-bellieds, and occasionally Common
Fig. 1. Map of Lake Placid study site showing winter territories of 9 juvenile (juv) and 8 adult (ad) Red-headed Woodpeckers and the home ranges of 4 Red-bellied Woodpeckers (RBW). Arrows indicate the oak patches known to be used by Red-headeds during the harvesting period. Large dots represent principal Red-headed storing posts.

Flickers (*Colaptes auratus*), fed from the same storage posts, and 3 times I saw all 3 species simultaneously on 1 stub. I could not be certain whether Red-headeds or Red-bellieds had originally cached the stores, or when, but I did see a few Red-headeds harvesting and storing acorns then. By 11 October, Red-headeds had spread out into individually occupied territories, and Red-bellieds had taken over the largely emptied storage posts.
### Table 1

**Sizes of 22 Red-headed Woodpecker Winter Territories in 2 Study Areas**

<table>
<thead>
<tr>
<th>Size Range (ha)</th>
<th>Number</th>
<th></th>
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</tr>
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<tbody>
<tr>
<td></td>
<td>Adults</td>
<td>Juveniles</td>
<td>Total</td>
</tr>
<tr>
<td>0.04–0.5</td>
<td>4</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td>0.5–1.0</td>
<td>2</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>1.0–1.5</td>
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<td>3</td>
<td>4</td>
</tr>
<tr>
<td>1.5–2.0</td>
<td>3</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>10</td>
<td>12</td>
<td>22</td>
</tr>
<tr>
<td><strong>Mean Size (ha)</strong></td>
<td>1.00</td>
<td>0.95</td>
<td>0.97</td>
</tr>
<tr>
<td><strong>SD (ha)</strong></td>
<td>0.20</td>
<td>0.37</td>
<td>0.30</td>
</tr>
</tbody>
</table>

**Winter territories.**—The main requirements for winter territories were the presence of dead trees for storage space, open vegetation for easy defense of the stored mast, and an abundant acorn supply nearby. Beyond these conditions, the woodpeckers showed no further preference for specific vegetation types. By late October, they were scattered in individual territories throughout the scrub (Fig. 1). Acorn-bearing oaks did not have to be within the woodpeckers' territories. As did Kilham (1958a) and Bock (1970, Lewis' Woodpeckers), I found birds harvesting acorns up to 100 m from their defended storage area. The woodpeckers did not defend their harvesting grounds, and individuals from different territories frequently harvested from the same oak patches (Fig. 1). This contrasts with MacRoberts' (1975) observation in Louisiana, where Red-headeds gathered mast only from within their territories.

I plotted the territories of 22 individuals, taking the boundaries to be the outermost trees or posts visited regularly by each bird during the study. The 17 territories in the primary study site are shown in Fig. 1. Although the territories varied considerably in size (Table 1), they were larger than the ones measured by Kilham (1958b; Maryland, average territory 0.1–0.2 ha) and apparently comparable in size to those studied by MacRoberts (1975; Louisiana, 0.8–1.2 ha). This further supports MacRoberts' view that territory size is compressible, probably correlated with the mast production of the habitat. While Kilham (1958a) found that adults held smaller, more easily defended, and more productive areas, I found no difference between adult and juvenile territory sizes (Table 1).

**Aggressive interactions.**—Red-headed Woodpeckers defended their territories against many species. Defense was most vigorous within the central
portion of their territory, where most of the stored cache and the roost hole were located (see also Kilham 1958b, MacRoberts 1975). All potential acorn robbers were chased, including Red-bellied Woodpeckers, Common Flickers, Scrub Jays (*Aphelocoma coerulescens*), and Common Grackles (*Quiscalus quiscula*). A few non-acorn feeders were also pursued such as American Robins (*Turdus migratorius*), Mockingbirds (*Mimus polyglottos*), Great Horned Owls (*Bubo virginianus*), and Red-shouldered Hawks (*Buteo lineatus*). In contrast, Loggerhead Shrikes (*Lanius ludovicianus*) were not only tolerated by the woodpeckers, but often were seen in close proximity, frequently using storage posts as hawking perches. These species did not seem to interact in any way. The single time I saw a Hairy Woodpecker (*Picoides villosus*) in the area, the shrike was even more aggressive and persistent than the Red-headed in chasing it away.

The rates of intra- and interspecific interactions throughout the study are summarized in Fig. 2. Each aggressive encounter was given an intensity factor, ranging from 0, when the birds were tolerated, to 3, when they grappled and fell to the ground. Bill-pointing and bobbing were given value 1: chasing and calling, 2. The average intensity of interactions for each species is given in Table 2, along with the percentage of acorns in the diet of Red-headeds and the species they interacted with. The table shows that the Red-headed aggression intensity increased with the degree of acorn consumption of the various species.

Intraspecific conflicts diminished markedly in October, once Red-headeds had established individual territories (Fig. 2). The few interactions I observed occurred along territorial boundaries. Twice I watched a bird lose an acorn it had stored just past the border of its territory. The woodpecker was chased away by its neighbor, which proceeded to store the acorn closer to the nucleus of its own territory. Such occurrences probably reinforce sharp territorial boundaries and induce the birds to store their mast toward the center of their territories. Intraspecific robbery is reported for Lewis’ Woodpeckers (Constantz 1974) but I never saw Red-headeds steal stored mast from an unguarded post.

Beginning in mid-November, intraspecific conflicts started to increase again, after diminishing almost to zero (Fig. 2). By this time Red-headeds were moving around their territories more, in pursuit of emerging insects (see Flycatching, below), which resulted in more conflicts along their boundaries.

Red-bellied Woodpeckers were vigorously chased throughout the study (Table 2). The Red-bellieds seemed to search for inattentive Red-headeds and a few times succeeded in stealing morsels of stored mast from Red-headed territories. But Red-headeds were usually alert, and quickly chased any Red-bellied that even approached their territories. Frequently, Red-bellieds were
Fig. 2. Frequency of inter- and intraspecific interactions of Red-headed Woodpeckers in defending their storage posts. The dashed line in this and in subsequent figures marks the establishment of individual territories.

persistent, making several return attempts before being finally expelled. Because their large home ranges included several Red-headeds' territories (see Fig. 1), Red-bellieds were able to return habitually to rob Red-headed storage posts. Red-bellieds do not keep close guard of their own stores, and this further facilitates their robbing behavior. When chased, Red-bellieds called loudly and flew away. I never saw them return a Red-headed’s attack.

Aggressive relationships between these species were not always clearcut; at times a Red-bellied was tolerated in areas from which it was customarily chased, or pursued from areas in which it normally roamed freely. The intruder’s activity probably had an effect on whether it would be ignored or pursued.

When given the opportunity, Red-bellieds took over their congener’s territory, and even though they had trouble extracting or finding a good portion of the stored mast, they eventually succeeded in depleting most of it. One
Red-headed territory, for example, was abandoned late in November, when its owner disappeared. The following day, a neighboring male Red-bellied pecked all over the former owner's stores. This Red-bellied's mate, a frequent intruder even while the Red-headed was present, attempted to join the male, but was vigorously chased and forced to search the peripheral posts. I saw both Red-bellies return on following days to eat the dwindling mast supply; I saw no Red-headed ever approach the area.

Florida Scrub Jay families held territories in both study areas. Conflicts with these birds occurred during a 2-week period just after the Red-headeds established winter territories. The fights were intense (Table 2), and normally involved several jays against a single woodpecker. After this brief period, however, Scrub Jays and Red-headeds occupied overlapping territories without aggression, even though acorns are also a major component of the jay's diet (Table 2).

Red-headed Woodpeckers were rarely successful in driving big flocks of robins or grackles away from their territories. The intruders ignored the woodpeckers' frantic calls, and only left after repeated attacks to the center of their flocks. Although the woodpeckers did not defend their harvesting grounds, they chased away any grackle approaching the oaks, possibly in response to the latter's large numbers. Mockingbirds were tolerated, and the few interactions I observed were very mild. Common Flickers were chased away at first, but later were mostly ignored. In the 2 conflicts I saw before winter territories were fixed, the flickers made several return attempts

---

**Table 2**

<table>
<thead>
<tr>
<th>Date</th>
<th>RHW2</th>
<th>RBW</th>
<th>Fl</th>
<th>SJ</th>
<th>Gr</th>
<th>Rb</th>
<th>Mb</th>
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<tr>
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<td>1.0</td>
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<td>—</td>
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</tr>
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<td>—</td>
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<td>—</td>
</tr>
<tr>
<td>Dec 15-31</td>
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<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Av. intensity</td>
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<td>2.0</td>
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<tr>
<td>No. months chased</td>
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<td>3</td>
<td>2</td>
<td>0.5</td>
<td>1.5</td>
<td>1.0</td>
<td>1.0</td>
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<tr>
<td>% acorns in diet2</td>
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<td>10-25</td>
<td>0.5-2</td>
<td>25-50</td>
<td>5-10</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

1 See text.
2 From Martin, Zim and Nelson (1951).

RHW = Red-headed Woodpecker; RBW = Red-bellied Woodpecker; Fl = Common Flicker; SJ = Scrub Jay; Gr = Common Grackle; Rb = American Robin; Mb = Mockingbird.
before being finally driven away by the Red-headed Woodpeckers. However, once the Red-headed Woodpeckers’ territories were set up, intruding flickers flew away immediately even at the call of the Red-headed. Flickers probably did not pose a serious threat to Red-headed Woodpeckers as their habits are markedly different and acorns account for only 1–2% of their diet.

Interspecific conflicts decreased progressively after November. This was seemingly caused by the Red-headed Woodpeckers’ increasing tolerance of the intruders, especially robins, which they rarely chased after November, and flickers, which they came to ignore (flickers were using Red-headed Woodpeckers’ posts as perches for courtship displays). Red-headed Woodpeckers also seemed less agonistic toward Red-bellieds, and a few times I saw the latter fly to Red-headed posts without provoking immediate attacks.

**TIME BUDGETS AND FORAGING BEHAVIOR**

*Harvesting and storing acorns.*—Figure 3 summarizes the foraging behaviors Red-headed Woodpeckers displayed during the fall and winter, illustrating the changes that occurred as the season progressed. Acorn related activities, which comprised the most important foraging event, are further broken down in Figure 4, which again shows the shifts in emphasis that developed during the study period. Harvesting, as described by Kilham (1958a), was the predominant behavior among Red-headed Woodpeckers during the first 10 days after establishing their territories. Shelling acorns and searching for suitable storage places were the most time consuming activities. Usually only 1 Red-headed visited a given harvesting area at a time. Clashes occurred only occasionally, and especially among juveniles or with grackles and Scrub Jays. Red-headed Woodpeckers maximized their harvesting time by only breaking the acorns in halves or by storing them whole when they found a sufficiently large crevice. Bock (1970) reports a similar behavior in the Lewis’ Woodpecker, although, unlike the latter, Red-headed Woodpeckers use special dead branches, not storing posts, as “anvils” for cracking their acorns. I observed sporadic harvesting well into the first half of December.

For acorn storage, Red-headed Woodpeckers used dead stubs, dead branches of living trees, and, in some cases, even trunks of living slash pines. They did not excavate their own storage cavities. Like the Lewis’ Woodpecker (Bock 1970), they used natural crevices and holes, occasionally enlarging a few (see also Kilham 1958a). I found only acorns, whole or in bits, stored in the holes. Kilham (1958a) also found a few insects when he inspected some of the storing branches.

Following the major harvesting period, the emphasis shifted to “re-storing.” As Kilham (1958a) and Pinkowski (1977) describe, the woodpeckers ex-
Fig. 3. Frequency of different types of fall and winter foraging behavior by Red-headed Woodpeckers expressed as percentages of total timed observations. In this and subsequent figures, the month of October is divided into three 10-day intervals: one before and two after the establishment of individual territories. Remaining months are divided into two 15-day intervals each. Horizontal bars show total percentage of time spent foraging during each period.

tracted their acorns, carried them to an anvil, and broke them into tiny morsels which they distributed over their storing posts. Two factors might help explain the energy invested in this behavior: (1) several of the storage posts were extremely rotten, and a few of them were blown down by strong winds; (2) whenever Red-headeds were inattentive, Red-bellieds, and occasionally Common Flickers, robbed their stores (see also Pinkowski 1977). Thus, as Kilham (1958a) suggests, it would have been precarious to store the entire harvest in one spot.

Shell-less morsels are open to fungus attack, and I found several stored pieces that were rotting. Red-headed Woodpeckers often climbed their storage posts, lightly and rapidly picking at almost every hole, and apparently not feeding. The birds may have been turning their acorn morsels to dry them out and minimize fungal infections as Bock (1970) suggests for the Lewis’
Woodpecker. This behavior may also serve to monitor the number of holes still filled with mast, determining whether or not to harvest more acorns.

Kilham (1958a) describes a habit of Red-headeds, apparently unique among the Picidae, of covering up storage holes with splinters of wood. MacRoberts (1975) and Pinkowski (1977) also report this phenomenon. Kilham observed this behavior after heavy rains, when the splinters were soft and manageable. Whenever I saw Red-headeds engaged in this behavior, they were using dry slivers, which they often had great difficulty fitting into the holes. The percent of time devoted to covering their stores increased greatly toward the end of December (Fig. 4).

It was difficult to estimate how much of the stored mast the Red-headeds were actually consuming. The birds usually ate bits of an acorn while pounding it, and I believe they also ate some while working over their stores. Until December, the birds ate mostly acorns they had just harvested, not ones they had extracted from storage. In February, feeding from storage
was much more common and obvious. The birds pounded at their holes and occasionally gleaned from their posts, eating the scattered bits of stored mast. When I checked some posts in May 1976, I found a few acorns still left in 8 of 10 stubs examined. After the winter of 1976–77, which was unusually cold, I found no mast remaining in any of the 6 posts I checked at the time the woodpeckers left their territories early in March.

**Flycatching and gleaning.**—Red-headed Woodpeckers devoted more time to flycatching once the active acorn harvesting period was over (Fig. 3). On warm days in November, December, and especially February, it was common to see all individuals in the population engaged solely in hawking flying insects.

Rarely, the woodpeckers gleaned from branches and trunks, or probed into clusters of ball moss (*Tillandsia recurvata*) and Spanish moss (*T. usneoides*), apparently catching surface prey. This type of foraging, in contrast, was the principal foraging mode displayed by Red-bellieds in the denser habitats that Red-headeds deserted in the fall. In the open scrub, where the 2 *Melanerpes* species co-existed during winter, *M. carolinus* gleaned limbs and posts much more frequently than did its congener.
Maintenance activities.—The amount of time spent foraging declined after the harvest period, when Red-headed Woodpeckers shifted to activities involved in maintenance and territorial defense. After the completion of roost holes in mid-November, maintenance consisted of quiet perching (Fig. 5). In February, 1977, I included most perching (76% of the total observation time) under “flycatching,” as the birds constantly looked around and sallied whenever an insect flew by. In both habitats, Red-bellieds’ maintenance activities also increased significantly after November, when the birds were no longer feeding their young.

Discussion

Red-headed Woodpeckers in south-central Florida stop feeding their young early in the fall and intraspecific aggression becomes progressively more intense until the groups split up into individual winter territories. They then spend the majority of their time harvesting acorns, flying almost continually into and out of their territories, from oaks to “anvil” to storage posts. This active phase is followed by a more sedentary “re-storing” phase, when the birds remain at their storage posts, rearranging their mast and chasing away intruders. During these first weeks on the winter grounds, only a small fraction of time is spent actually feeding or resting. Thus, as in Lewis’ Woodpeckers (Bock 1970), Red-headed Woodpeckers (Bock 1970), Red-headed Woodpeckers in Maryland and Louisiana, also reveal their close dependence on acorn crops in selecting their winter grounds. However, Willson’s (1970) and Reller’s (1972) observations of these woodpeckers in Illinois imply a very different behavior in that area. Willson describes the Red-headed Woodpeckers as “generalist” feeders, and Reller found that they were selective in their choice of species and portions of trees in which to forage, which suggests that they gleaned a large portion of their diet, relying less on mast. Willson and Reller found that M. erythrocephalus and M. carolinus segregated in feeding sites, and neither mentions differences in foraging techniques. However, in my study, the primary foraging mode observed for Red-bellieds was gleaning and probing (see also Stickel 1965, Kilham 1963), activities that Red-headed Woodpeckers rarely
engaged in. Pinkowski (1977) reports storing and re-storing behavior of Red-headeds during the summer in Michigan, which suggests that at least in part of their northern range, Red-headeds show their specialized foraging habits year-round.

Accounts (Kilham 1958b, Reller 1972) regarding Red-headeds' aggressive behavior agree with my findings in Florida: (1) Intraspecific conflicts drop drastically once winter territories are set up, and (2) Red-bellieds are major competitors of Red-headeds. I did not observe the agonistic interactions between Red-headeds invading each other's territories described by Kilham (1958b). This probably reflects the lower densities of Red-headeds in my study area (see also MacRoberts 1975).

Red-headed Woodpeckers seem to have specialized in their diet such that all of their seasonal activities revolve around it. Thus in the fall they must look for and move into suitably open, acorn-bearing habitats. Their behavior throughout the winter revolves around use and defense of their stored mast. In contrast, Red-bellieds have generalized foraging tactics, using a slight specialization in morphology. Their unusually versatile tongue allows them to reach and manipulate objects in holes and crevices to which most other birds have no access (Kilham 1963). With a more diverse diet, and no need to keep constant guard of their stores, Red-bellieds do not undergo the major shifts in behavior that are associated with the Red-headeds' local migrations into individual, specialized winter territories.

Because individual Red-headed and Lewis' woodpeckers do not necessarily return to the same winter territories each year, their winter foraging and territorial behavior is oriented toward short-term exploitation of their habitat. Cracking and fitting acorns into natural crevices requires considerably less energy than drilling holes for whole-acorn storage in special "granaries." The risk of losing the cracked pieces to fungal rot is of little consequence for the 2 migratory species, as they depart from their territories and any remaining stores after a few winter months. In contrast, Acorn Woodpeckers may eat stored mast throughout the year (MacRoberts and MacRoberts 1976), hence it is to their advantage to spend the extra energy in keeping their stores edible for longer periods.

Aspects of short-term residency can also be seen in the different harvesting strategies. Red-headed Woodpecker families break up in the fall, and individuals simultaneously exploit the superabundant acorn crop as rapidly as possible. They do not defend the productive oak patches, but instead concentrate on quickly accumulating sufficient stored mast for their own winter use. Furthermore, except for the relatively brief harvest period (Fig. 4), they are not likely to return to the same area in the near future. Acorn
Woodpeckers, on the other hand, hold territories in habitats that are annually predictable, and that meet requirements for both winter and summer (MacRoberts and MacRoberts 1976). As a result, they defend their harvesting areas, in order to assert permanent dominance within these productive habitats.

The contrast in the social structures of the 3 mast-consuming *Melanerpes* species is again related to this permanent vs. short-term residency. Red-headed and Lewis' woodpecker individuals disperse to provide for themselves in unpredictable habitats, while Acorn Woodpecker groups remain intact and cooperate in mast storage, roost and granary maintenance, and defense of their permanent territories.

Red-headed and Lewis' woodpeckers have dull juvenal plumage lasting well into the winter, while immature Acorn Woodpeckers resemble adult males (Spray and MacRoberts 1975). The different Red-headed juvenal plumage presumably contributes to diminishing aggression from adults. The fact that juveniles engaged in fights among themselves considerably more often than did adults might also suggest that the bright pattern of the adults' plumage is itself an effective signal for territoriality. However, this bright head color is apparently effective mostly intraspecifically, as juveniles seemed to have no more trouble than adults keeping intruders away. The difference in juvenal plumage patterns may also be related to the difference in social systems among the 3 species. Juvenile Red-headed Woodpeckers may benefit from decreased aggression by adults during the establishment of individual territories, while, by resembling adults, young Acorn Woodpeckers may be more effective in the cooperative defense of the group's territory.

**SUMMARY**

I studied foraging and territorial behavior of Red-headed Woodpeckers in south-central Florida. In autumn the birds leave their breeding territories and migrate to productive patches of oak scrub, arriving as acorn crops mature. Each individual establishes a separate territory within open scrub habitat and defends an area surrounding several dead trees, which it uses for storing acorns and excavating roost holes. Behavior patterns change markedly as the winter season progresses: most of early autumn is spent harvesting mast, which is then rearranged and covered during late fall. Flycatching predominates on suitable days in mid-winter, and the bulk of the stored mast is consumed only in late winter. Both intra- and interspecific aggressive behavior changes with the progression of different foraging activities throughout the season.

Red-headed Woodpeckers resemble the congeneric Lewis' and Acorn woodpeckers in their dependence on mast harvesting and storage. Opportunistic Red-headed and Lewis' woodpeckers depend on sporadically abundant crops, and show specialized winter behavior associated with their seasonal movements. In contrast, Acorn Woodpeckers occupy habitats with more reliable acorn supplies, and the species is resident and highly social all year.
ACKNOWLEDGMENTS

I thank the late Mr. Richard Archbold for making available all the facilities at the Archbold Biological Station, and for supporting my stay there. James N. Layne and students visiting the Station were helpful with advice and support. I am sincerely grateful to Dean Amadon, Henry S. Horn, James N. Layne, Fred E. Lohrer, John W. Terborgh, and Glen E. Woolfenden for their constructive comments on the manuscript, and I owe special thanks to John W. Fitzpatrick, for his time, effort, and patience in reviewing and criticizing various versions of the manuscript.

LITERATURE CITED


ARCHBOLD BIOLOGICAL STATION, RT. 2, BOX 130, LAKE PLACID, FL 33852. ACCEPTED 20 DEC. 1977.
TARSAL COLOR OF AMERICAN COOTS IN RELATION TO AGE

RICHARD D. CRAWFORD

Gullion (1952) suggested from data collected on 14 captive individuals that tarsal color of juvenile American Coots (*Fulica americana*) was blue- or gray-green, yellow-green in yearlings, and yellow, yellow-orange, or red-orange in older adults. Burton (1959) examined tarsal colors of 970 coots and suggested that many yearlings have green tarsi. While studying age-specific breeding biology of American Coots in northwestern Iowa during 1972–1974, I collected data on tarsal color relative to age. Coots were studied at Dan Green Slough and Dewey’s Pasture, 2 glacial marsh systems described by Sooter (1941) and Bennett (1938), respectively. This paper includes an analysis and discussion of the tarsal color variation I observed.

METHODS

Breeding and nonbreeding coots were captured by several methods (Crawford 1977) and were banded with U.S. Fish and Wildlife Service leg bands and color-marked with nasal saddles (Sugden and Poston 1968). All trapped birds were placed in 1 of 5 age classes based initially on Gullion’s (1952) tarsal color scheme. Photographs were taken of the lateral side of the tarsus of each bird, and tarsi of all individuals retrapped in subsequent years after banding were again photographed with the same type of film. Tarsal colors were described qualitatively in the field immediately after each individual was captured. More precise designations of color were later taken from the slides.

Thirty-three individuals of various ages were placed in captivity at the Ledges Research and Exhibit Station, Boone, Iowa, in August 1972. Tarsal color changes of 18 of these birds were observed until May 1974.

RESULTS

I will first describe my aging scheme by using the qualitative color descriptions of Gullion (1952). I will then describe the various colors precisely by using a standard color code.

*Tarsal color changes of free-living coots.*—I banded and color-marked 334 coots, of which 22 (14 females and 8 males) were retrapped in later years (Table 1). On the basis of observations on these individuals, plus data from Gullion (1952) and Burton (1959), the study populations were redivided into 5 age classes (Table 2). Age-class 0 represents juveniles the same summer they hatched. I found that the tarsal color of newly hatched coots is tan and that by 30–45 days of age the tarsal color has changed to blue-
Crawford • COOT TARSAL COLOR

Table 1
TARSAL COLOR CHANGES OBSERVED IN FREE-LIVING AMERICAN COOTS

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<td>G</td>
<td>YG</td>
<td>G</td>
</tr>
<tr>
<td>1</td>
<td>female</td>
<td>YG</td>
<td>YG</td>
<td>YG</td>
</tr>
<tr>
<td>3</td>
<td>male</td>
<td>YG</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>2</td>
<td>female</td>
<td>YG</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>1</td>
<td>male</td>
<td>YG</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>1</td>
<td>female</td>
<td>Y</td>
<td>YO</td>
<td>YO</td>
</tr>
<tr>
<td>1</td>
<td>female</td>
<td>Y</td>
<td>YO</td>
<td>YO</td>
</tr>
</tbody>
</table>

¹ BG = Blue-green, G = Green, YG = Yellow-green, Y = Yellow, YO = Yellow-orange.

green. Age-classes 1, 2, and 3 represent probable age in years, and age-class 4 includes all birds believed to be 1 year old or older.

Twenty-one of the 22 returns in Table 1 (96%) showed color changes consistent with the age classes established in Table 2, and both male and female coots showed similar changes. Only 1 bird returned in 2 successive years. This bird was a juvenile with blue-green tarsi when trapped in 1972 and returned in 1973 with green tarsi and in 1974 with yellow-green tarsi.

Tarsal color changes of captive coots.—The 18 captive coots were trapped in July, and tarsal colors were checked monthly until the following May. By late August, changes in tarsal color of some of the birds were evident.

Table 2
AGE CLASSES OF AMERICAN COOTS BASED ON TARSAL COLOR

<table>
<thead>
<tr>
<th>Age-class</th>
<th>Probable Age (years)</th>
<th>Tarsal Color</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Juveniles (&lt;90 days old)</td>
<td>Tan to blue-green</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>Green</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>Yellow-green</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
<td>Yellow</td>
</tr>
<tr>
<td>4</td>
<td>4 or greater</td>
<td>Yellow-orange to red-orange</td>
</tr>
</tbody>
</table>
and by late September, the tarsal color of all adults had faded from the vivid colors typically found during the breeding season (Table 3). By late September, tarsal colors of age-classes 0 and 1 were indistinguishable. No change in tarsal color was noted from September through May, and none of the birds regained their normal tarsal color by the following May.

**Description of tarsal colors.**—Gullion (1952) assigned qualitative color descriptions to the coot tarsi in his study (e.g. blue-green). Because these descriptions do not necessarily correspond to notations used in standard color codes, I will describe more fully the colors found on the tarsi by using a standard color code. Smithe’s (1975) system used swatch color names (e.g. olive-gray) with corresponding swatch color numbers (e.g. 42). He also gave corresponding Munsell notations for his swatches. The Munsell system involves numerical specification of colors (e.g. 6/2 7.5Y = Value/Chroma Hue). Wood and Wood (1972) explained the utility of the Munsell system to avian study. The following age-class descriptions give the color used by Gullion (1952), swatch color name and number used by Smithe (1975), and the Munsell notation also taken from Smithe.

- **Age-class 0 (juvenile)**—Blue-green of Gullion; using Smithe’s color code, grayish olive (43, 5/2.5 5Y) to yellowish olive-green (50, 4.5/6 8Y) on the leading edge of the tarsus fading into olive-gray (42, 6/2 7.5Y) or plumbeous (78, 4/1.5 5PB) on the trailing edge.

- **Age-class 1 (1-year-old)**—Green of Gullion; using Smithe, olive-green (46, 4/4 8.5Y) to yellowish olive-green over entire tarsus.

- **Age-class 2 (2-year-old)**—Yellow-green of Gullion: using Smithe, entire tarsus olive-yellow (52, 7/7 7.5Y), or spectrum yellow (55, 8.5/12 6Y) on leading edge of tarsus fading into yellowish olive-green on trailing edge.

- **Age-class 3 (3-year-old)**—Yellow of Gullion; using Smithe, entire tarsus spectrum yellow.

- **Age-class 4 (4-year-old or older)**—Yellow-orange or red-orange of Gullion; following Smithe, tarsus with a base color of spectrum yellow or orange-
yellow (18, 8/14 10YR) with spots of chrome orange (16, 6/16 2.5YR) or flame scarlet (15, 5/16 10YR). Tarsal colors evidently tend to become almost entirely chrome orange or flame scarlet as the coots get older (Gullion 1952).

Most field biologists will have little difficulty distinguishing tarsal colors of trapped birds. The differences between age-classes 1 and 2, however, can be difficult to discern for some individual coots. Based on my observations, most age-class 1 birds will have tarsal colors distinctly greener than those in age-class 2. When the differences are slight, another criterion might be used as an aid to classification: Of 42 age-class 1 birds I examined, only 5 had red-orange color on the distal end of the tibia, but 36 of 38 age-class 2 and all older coots showed this characteristic.

Field determination of tarsal colors while coots are standing out of water is possible, but should be attempted only after experience with trapped individuals. I found that color determinations made in the field under conditions of poor light and visibility were often incorrect.

Because Gullion's (1952) color descriptions have been used elsewhere (Burton 1959, Giles 1969), I suggest continuing use of these color names in future work, but future users should be fully aware of the above descriptions when interpreting the color names used.

**DISCUSSION**

*Tarsal color changes.*—Twenty-one of 22 free-living coots showed color changes consistent with the aging scheme proposed (Tables 1 and 2). My aging scheme is similar to that proposed by Gullion (1952), except that his system is 1 year behind mine (i.e. he suggested that juveniles had blue-green or green tarsi and yearlings had yellow-green tarsi). Gullion (1952) based his aging scheme primarily on 14 individuals that he captured in October and January and for which he traced tarsal color changes through the following July. He stated (p. 192) that "11 of the 14 birds, when originally taken, had gray-green legs like 90-day-old immatures." I have shown (Table 3) that apparently both juvenile and 1-year-old coots have gray- or blue-green tarsi during the fall and winter periods. In addition, Gullion (1954: 396) stated that juvenile coots 4–5 months old cannot be distinguished from adults by plumage characteristics alone. The possibility exists, therefore, that he captured 1-year-old coots rather than juveniles as he had suspected. If this is true then our aging schemes are completely compatible.

Other evidence exists to suggest that yearling coots have green tarsi rather than yellow-green during the breeding season. I found that approximately 57% of May–July populations had green tarsi (Crawford 1975): one would
expect the yearling cohort to be more numerous than older cohorts. Burton (1959) examined tarsal colors of 970 coots, some of which were killed by hunters during October and some of which were accidentally caught in muskrat traps in November; he suggested that many yearlings have green tarsi. His data are difficult to interpret, however, because he used birds captured during the fall and winter, the time when ages seemingly are difficult to distinguish by tarsal colors alone. Kornowski (1957) and Blums (1973) found that yearlings of the similar European Coot (\textit{Fulica atra}) had gray or green tarsi and that older adults had yellow, orange, or red tarsi. Some of the disparity might be related to semantics used in describing colors.

Testosterone has been shown to cause soft part color changes in several species (Witschi and Miller 1938, Noble and Wurm 1940, Witschi 1961); some exceptions, however, have been noted (Witschi 1955, Lofts and Murton 1973, Lofts et al. 1973). I hypothesize that testosterone or a similar derivative causes color changes in coot tarsi because both sexes show similar color changes. If testosterone is influencing tarsal color in coots, it seems likely that tarsal colors would be more vivid during the breeding season because testosterone secretion is known to increase in at least some species at this time (Assenmacher 1973, Lofts 1975). In addition, Trauger (1974) suggested that testosterone was influencing fall or winter regression or darkening of female Lesser Scaup (\textit{Aythya affinis}) iris color. Seasonal changes in tarsal color were shown for captive coots in this study (Table 3) and suspected for at least 1 wild bird (Table 4). On the basis of these observations, I recommend that the tarsal color aging scheme outlined here be used only during the breeding season. Perhaps additional study will further elucidate tarsal color changes during the nonbreeding season.

The fading of the tarsal colors of captive individuals also might explain why 1 female wild bird had yellow-green tarsi in both 1972 and 1973. She was captured in July 1972 while incubating, but not again until August 1973, apparently after she had nested.

Little use has been made of tarsal colors as indicators of age in studies of other birds. Shortt (1943) used tarsal color for age discrimination of Black Ducks (\textit{Anas rubripes}). Table 4 presents evidence from other authors to suggest that a range of tarsal colors similar to that found in the American and European coots occurs in the Sora (\textit{Porzana carolina}), Purple Gallinule (\textit{Porphyrylula martinica}), and Common Gallinule (\textit{Gallinula chloropus}).

Behavioral significance of tarsal color variability.—Further study is needed to determine the behavioral significance, if any, of variable tarsal colors to coots. Two possibilities, however, will be mentioned. (1) Bright colors often are used to indicate dominance in many species. Older adult male Red-winged
Table 4

Variation in Tarsal Color of Other Rallidae

<table>
<thead>
<tr>
<th>Species</th>
<th>Tarsal Color</th>
<th>Authority</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sora</td>
<td>Green</td>
<td>Samuels (1867)</td>
</tr>
<tr>
<td></td>
<td>Yellow-green</td>
<td>Ridgway (1941)</td>
</tr>
<tr>
<td>Purple Gallinule</td>
<td>Green</td>
<td>Coues (1903)</td>
</tr>
<tr>
<td></td>
<td>Yellow-green</td>
<td>Forbush (1925)</td>
</tr>
<tr>
<td></td>
<td>Yellow</td>
<td>Pearson (1923)</td>
</tr>
<tr>
<td>Common Gallinule</td>
<td>Green</td>
<td>Chamberlain (1891)</td>
</tr>
<tr>
<td></td>
<td>Yellow-green</td>
<td>Reilly (1968)</td>
</tr>
<tr>
<td></td>
<td>Yellow</td>
<td>Coues (1903)</td>
</tr>
</tbody>
</table>

Blackbirds (*Agelaius phoeniceus*), for example, are more brightly colored than yearlings. Nero (1956) suggested that this brighter color was used to the older male’s advantage in territorial establishment and defense. Both male and female coots participate in territorial defense (Gullion 1953), and limited data indicate that coots use their feet in fighting so that the tarsi are visible above water for short periods of time (pers. observ.). Thus, tarsal color might be used to indicate dominance among both males and females. (2) Females of most bird species normally choose their partner and often rely on visual cues for recognition (Lofts and Murton 1973). I do not know if female coots choose their mates, but if they do, they may use tarsal color of males in this process.

SUMMARY

Data obtained from 22 color-marked coots recaptured in years subsequent to their banding indicate that during the breeding season yearling coots have green tarsi, 2-year-old coots have yellow-green tarsi, 3-year-old birds have yellow tarsi, and all older coots have tarsi ranging from yellow-orange to red-orange. Discrepancies between this aging scheme and ideas expressed by earlier workers are discussed. Data from captive coots indicate that tarsal colors fade outside of the breeding season. I recommend that without further study the aging scheme described be used only during the breeding season. The possible behavioral significance of age-specific tarsal color in coots is discussed.

ACKNOWLEDGMENTS

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LITERATURE CITED


Crawford • COOT TARSAL COLOR 543


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NESTING BEHAVIOR AND AFFINITIES OF MONK PARAKEETS OF SOUTHERN BUENOS AIRES PROVINCE, ARGENTINA

PHILIP S. HUMPHREY AND ROGER TORY PETERSON

The Monk Parakeet (Myiopsitta monachus) is an abundant bird in much of Argentina from Mendoza, Río Negro, La Pampa, and Buenos Aires provinces north into Uruguay, Paraguay, southeastern Brazil, Mato Grosso, and southern Bolivia. These noisy and highly social parakeets are of interest because of their nest building habits, unique in the family Psittacidae. Nests of Monk Parakeets are usually multi-chambered structures involving several pairs of birds. We encountered the Monk Parakeet in the southern “pan-handle” of Buenos Aires province nesting in a manner very different from the typical nesting behavior for the species.

On 26 October 1960 we drove from Bahía San Blas (southern Buenos Aires province) to Viedma, passing through the communities of José C. Casás and Cardenal Cagliero. We saw small numbers of Monk Parakeets along a short stretch of road between these towns. We collected a few specimens, noted what we thought might be nests on the tops of telephone poles, and hurried on to Viedma. These birds were smaller and less yellow than specimens we had collected near Chascomus in northern Buenos Aires province. Two days later we made further observations of these parakeets.

Buenos Aires province has its southernmost extension in the form of a narrow panhandle of dry, semidesert country along the Atlantic coast. The southern two thirds of this panhandle, that is, the part south of the Río Colorado, is a region of thorny scrub vegetation and occasional large depressions that look like gleaming white lakes but are actually great expanses of dry lake beds. This part of Buenos Aires province is in the phytogeographical province termed Monté by Solbrig (1976:10-12) and others.

During the 2 days that we studied the parakeets in southern Buenos Aires province we found the birds 21 km southwest of Casás in a limited area along 2.3 km of the road. There were 35 telephone poles along this stretch of road; 9 of these had bulky stick nests between the crossbars at the top. Some of these nests were occupied by Firewood Gatherers (Anumbius annumbi) or were abandoned nests of this furnariid. Three of the nests were very much enlarged and consisted in part of freshly-added, large, thorny branchlets.

There were at least 13 parakeets in this small area. Birds were seen often in pairs or in flocks of from 3 to 5, and once, 9. At one time or another
we saw parakeets climbing about and peering into each of the 9 nests. The birds never moved far from the telephone lines and seemed to show considerable interest in large, nest-like structures on several of the telephone poles.

We thought there might be some relationship between the abundance of *Anumbius* nests and the local distribution of parakeets. A 26 km long census of *Anumbius* nests per kilometer of telephone poles (15 poles per km) revealed that they varied in abundance from 1 nest per 6 km to as many as
7 nests per km. The parakeets occurred in an area of average abundance of *Anumbius* nests (between 3 and 4 per km). Although there were *Anumbius* nests located in low thorn trees we saw no indication that the parakeets showed any interest in them.

Typical nests of the Monk Parakeet are multi-chambered structures involving sometimes as many as a hundred pairs of birds (Naumburg 1930:123). The fact that in southern Buenos Aires province the parakeets were attracted to *Anumbius* nests aroused our curiosity and led us to investigate these structures.

We climbed 3 telephone poles to bring down nests for closer examination. Each telephone pole was an old, rusty railroad rail with 2 wooden crossbars bearing insulators for the wires. The lower crossbar was approximately 6 m from the ground. All of the nests rested on the lower crossbar to one side of the pole and more or less filled the space between the crossbars.

The first 2 nests were old-appearing structures made of dried sticks. Each *Anumbius* nest was a bulky structure composed of fairly brittle dead twigs lacking large thorns. We felt that the nest material could have been collected from the ground litter. At the center of each nest was a small cavity approximately 15 cm in diameter; this was reached by a short entrance tunnel from one side. The total distance from the entrance to the inner wall of the nest cavity was approximately 40 cm. The nest cavity had a messy lining of dirty tufts of wool and other matter, including objects which looked like dried fox scats.

The third nest was much larger (approximately 50 X 70 cm) and was made mostly of fresh thorn branches which appeared to have been chewed off recently, presumably by a parakeet. These branches had new leaves sprouting from them. The branches were 20 to 40 cm in length and had long, sharp thorns. We later examined some of the thorny shrubs in the area and noted that the tips of many of the branches had been chewed off. The nest cavity contained a single Monk Parakeet egg. Further examination of this nest revealed that it was actually a double structure consisting of an *Anumbius* nest at one end and a parakeet nest at the other. The parakeet nest, however, engulfed the *Anumbius* nest, leaving no doubt that *Anumbius* had built the original nest. Part of the *Anumbius* end of the double structure was devoid of long, fresh, thorny branch-tips. The *Anumbius* and parakeet nests each had its own separate inner cavity and entrance tunnel. There was a double wall separating the nest cavities, and the entrance tunnels were at opposite ends of the duplex structure. The entrance to the parakeet's nest was to the north, forming the mouth of the roughly retort-shaped structure; the tunnel giving access to the *Anumbius* nest was at the south end and opened towards the west.
The inside diameter of the entrance tunnel of the parakeet's nest was approximately 10 cm and the distance from the entrance to the inner wall of the nest cavity was approximately 35 to 40 cm. The outside diameter of the nest at the entrance was approximately 25 cm. The nest chamber was 18 cm in diameter and was devoid of any lining although the stems of branches forming the chamber were in part divested of bark and seemed slightly smaller in diameter than those used for the outside of the nest.

Another nest constructed largely of green vegetation appeared to be about the same size as the one we took down and examined in detail. Its entrance, however, opened to the north.

Of the 9 nests around which we noted parakeet activity, 3 had had fresh plant material added to them and had been transformed into duplex structures comprising an original *Anumbius* nest more or less enveloped by an added parakeet nest. Various individuals or groups of parakeets were seen to visit only 9 nests. Parakeets were never seen at nests on telephone poles further north or south along the road.

On 23 October Peterson set up a blind approximately 11 m from an *Anumbius* nest and spent 2 h in it. The nest had not been added to by the parakeets but their interest in it and in the other *Anumbius* nests leads us to believe that building activities may have been about to begin.

Soon after the blind had been erected 2 parakeets arrived, and shortly afterwards a third. They first perched on wires near the nest where they showed obvious signs that they were aware of the blind, then 2 of the birds flew to a perch behind the nest. From time to time a parakeet's head would appear from behind the nest as if to study the situation. After several minutes all 3 birds flew off; they (presumably the same 3) returned 10 min later to perch about 2 m from the nest.

With sidestepping motions the birds moved along the wires to the nest, calling and "talking" a great deal in the process. Once at the nest one bird quickly entered while another went to the other side of the nest where he was hidden from sight. The walls of the nest were thin and Peterson could see the parakeet moving about within the nest cavity as if fiddling with the interior. This bird spent a long time in the nest before reappearing, at which point all 3 birds flew away. This routine was repeated several times during the 2 h Peterson spent in the blind. During this time Peterson did not observe any material being added to the nest nor did he see an *Anumbius* at the nest.

**TAXONOMIC NOTES**

There are 3 races of *Myiopsitta monachus* known from Argentina: *Myiopsitta m. monachus* from northern and northeastern Buenos Aires province,
VoL 4 Min. 110.0 112.5 Table 124.4 93.1 %7:451 and 7 Females Min. found eastern catita as valley mine. southern north. length about northeastern Choel, catita the birds from Myiopsitta La-Mendoza, 15 from Entre Cordolia, Choel-Mendoza, 15 specimens Myiascoinus (3iascoinus). In January 1961 Humphrey saw 2 Myiopsitta sitting on a telephone wire in southeastern La Pampa province between the town of Río Colorado and the border between the provinces of La Pampa and Buenos Aires.

Monk Parakeets in the southern panhandle of Buenos Aires province, northeastern Río Negro, and adjacent northeastern La Pampa province are about 600 km south of the known ranges for catita and nominate monachus. What then are the affinities of these southern parakeets?

Our specimens from Casás are about 20 to 30 g lighter in weight (Table 1) than specimens of monachus from Chascomus (Buenos Aires province) and Entre Ríos province, and have smaller bills and shorter wings. In addition, the abdomen is less yellowish and the dorsum duller green. The tails of the southern birds probably are shorter, but wear makes this difficult to determine. The Casás specimens are intermediate in wing (Table 2) and tail length between catita and nominate monachus, but indistinguishable from catita in plumage coloration. Therefore, we believe that Monk Parakeets from southernmost Buenos Aires province and the adjacent areas of southeastern La Pampa and northeastern Río Negro are Myiopsitta m. catita.

The range of catita appears to be within or mostly within the Monté region as characterized by Solbrig (1976:10–12) from the valley of the Río Negro north. The other forms of Myiopsitta also appear to be related to phyto-
Table 2

Wing Measurements (mm) of Monk Parakeets*

<table>
<thead>
<tr>
<th></th>
<th>Males</th>
<th></th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Min.</td>
<td>Mean</td>
<td>Max.</td>
</tr>
<tr>
<td>cotorra</td>
<td>20</td>
<td>132</td>
<td>136</td>
</tr>
<tr>
<td>monacha</td>
<td>23</td>
<td>135</td>
<td>148</td>
</tr>
<tr>
<td>catita</td>
<td>9</td>
<td>132</td>
<td>135</td>
</tr>
<tr>
<td>Casás specimens</td>
<td>7</td>
<td>133</td>
<td>140</td>
</tr>
</tbody>
</table>

* Specimens of cotorra from Brazil, Paraguay, Argentina (Formosa, Salta); monacha from Brazil, Uruguay, Argentina (Santa Fé, northern Buenos Aires, Entre Ríos); catita from Argentina (Tucumán, Santiago del Estero, Mendoza, San Luis).

geographical regions, i.e., nominate monachus in the Pampa region and cotorra in the Chaco (see map in Solbrig 1976:11).

**DISCUSSION**

In much of its range, the Monk Parakeet occurs in local populations numbering in the hundreds or even thousands, and builds large nests occupied by more than one pair of birds. There is considerable variation in size of nests and in kind of nest site selected. Moreover, the nest building habits of Monk Parakeets not only are adaptable to the availability of appropriate nest sites, but also are responsive to persecution. Finally, other species of birds and at least one species of mammal frequently are associated with parakeet nests. In spite of the economic importance of Monk Parakeets in Argentina (and elsewhere), there is little published information on their nesting habits.

The Monk Parakeet population near Casás is the only one known in which duplex nesting occurs with Anumbius. What are the characteristics of southern Buenos Aires province and of the parakeets themselves that might account for their unusual nesting habits in the vicinity of Casás?

The vegetation in much of southern Buenos Aires province south of the Río Colorado is principally scattered thorny shrubs and low thorny trees, most of which did not appear to be promising nesting sites for parakeets. Nevertheless, some of the taller trees might have provided appropriate sites. The only sites used, however, were the crossbars of telephone poles 6 m above the ground. None of the trees in the vicinity provide stable nest sites that high above the ground. We suspect that possibly marginal conditions along the southern and southeastern edge of the range of the Monk Parakeet might well affect the nesting behavior of the species.
In localities in the United States such as North Carolina where "numerous individuals, pairs, and large flocks have been observed" (Simpson and Ruiz 1974:171), the records suggest occupancy of nests by single pairs of parakeets or small numbers of pairs. "Breeding pairs, with typical bulky nests located in silos and on utility or telephone poles, have been observed in Barnardsville, with two nests in 1972 and two in 1973, and in West Asheville, with two nests in 1972 and one in 1973" (Simpson and Ruiz 1974:171). Bull (1973:504) notes that "two (once as many as six) pairs seem to be the maximum..." in the United States. Gochfeld (1973:264) states that "two to four pairs is the usual number in the New York area." However, Roscoe et al. (1974:21) reported a Long Island nest that housed 7 pairs. We hypothesize that "pioneer" Monk Parakeets in the U.S. start nesting activities in the northern hemisphere fall (austral spring) and that upon subsequent adjustment of their nesting cycles to the northern hemisphere seasons, they develop family colonies that build nests occupied by larger numbers of pairs.

Throughout their range, Monk Parakeets show wide variation in selection of nest sites. In part this variability is related to the availability of suitable trees and in part it is in response to relentless persecution of the parakeets, particularly in Buenos Aires province but also in other parts of their range. Earlier descriptions of the nesting habits of Monk Parakeets in Buenos Aires province mentioned that the preferred nest sites were in tala (Celtis spinosa) trees (Daguerre 1936:281; Orfila 1937:379–380; Dabbene 1918:112).

Daguerre (1936:282) found 3 colonies of Monk Parakeets on Isla Martín García, all of which had built their nests at great heights in eucalyptus trees. Two years earlier, one of the colonies had nested in the lower branches, which had been cut, the nests dumped, and the young removed. As a result, the parakeets renested higher in the eucalyptus where the nest could be destroyed only by cutting down the tree. Daguerre learned of a similar instance in Dolores (Buenos Aires province) where the parakeets, nesting in the low branches of tala trees, had had their nests burned out and subsequently began nesting high in eucalyptus trees. The fact that Monk Parakeets continue to persist in Argentina in spite of the determined efforts of the government to reduce by various means (including netting, fire, dumping of nests, poison) their depredations on corn and other crops, reflects the adaptability or flexibility of their nesting habits.

In southern Buenos Aires province, the habit of nesting on telephone poles instead of in the branches of the low trees in the Monté vegetation may be related both to the shortage of appropriate nesting sites and to the nesting habits of Anumbius.

Gibson (1880:5) noted of Monk Parakeets that "the new nests consist only of two chambers, the porch and nest proper, and are built and inhabited by
a single pair of birds. These become gradually added to, till plenty of them come to weigh perhaps a quarter of a ton each and are of a bulk enough to fill a large cart. Thorny tala twigs (no branches), firmly interlaced, form the only material . . .” Dabbene (1918:112) stated that Monk Parakeets nest colonially, building at first a single nest to which others are attached so that altogether they form an enormous mass of interlaced sticks of more than 1.5 m in height and the same in width suspended from the topmost branches of tala trees.

Apparently, the multiple or colonial nest of Monk Parakeets starts off with a single nest which forms a nucleus for—and a stimulus for—the construction of additional nests attached to it. In short, the colony does not start collectively to build a multiple nest; instead, it requires the initial stimulus of a first nest. We suspect that in the southern panhandle of Buenos Aires province, the bulky stick nests of Anumbius are surrogate first parakeet nests around which there is room only to attach a second nest. The only 3 parakeet nests we saw in southern Buenos Aires province were in association with Anumbius nests.

In other parts of their range, Monk Parakeets have nesting associates, principally a teal (Anas flavirostris), tree ducks (Dendrocygna) (Friedmann 1927:177), and an arboreal opossum. But these and possibly other species are associated with the parakeet nests secondarily rather than having been the initial stimuli for their construction.

The only other instance known where the parakeets build their nests in association with the nest of another species was mentioned by Naumburg (1930:128) who commented that “infrequently, the construction of new brood-chambers begins at the top, the structure being built downward from the bottom of the jabiru stork’s (Jabiru mycteria) nest, which forms a roof over all.”

SUMMARY

A small colony of Monk Parakeets (Myiopsitta monachus catita) was found in the Monté region of the southern panhandle of Buenos Aires province near José S. Casás in October 1960. The parakeets constructed nests on telephone poles in association with the nests of Firewood Gatherers (Anumbius annumbi). Each duplex nest consisted of an Anumbius nest to which parakeets added a nest of their own; the latter included a separate nest cavity and entrance tunnel constructed of freshly cut thorny branchlets. The Anumbius nests appeared to provide the stimulus for nest building by the Monk Parakeet.

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LITERATURE CITED


MORPHOLOGY OF THE LARYNX OF CORVUS BRACHYRHYNCHOS (PASSERIFORMES: CORVIDAE)

WALTER J. BOCK

The bones and muscles that support and control the opening of the glottis are among the poorest known parts of the avian skeletomuscular system. These features are either not mentioned in avian anatomical texts (e.g., Beddard 1898), or are described without illustrations (e.g., Gadow 1891:718, George and Berger 1966:264) or are described with inadequate figures (e.g., Schufeldt 1890:45, Edgeworth 1935:175–176, Fisher and Goodman 1955:36). White (1975:1891–1897) summarized the knowledge of the morphology of the larynx in domesticated birds and provided references to the veterinary anatomy literature; however, his descriptions are hard to use because of difficulties in correlating his terminology for the muscles with that used in the zoological avian anatomical literature. In all these cases, the descriptions are so vague or incomplete that it is not possible to visualize the configuration of the structures or to understand how the muscles operate to open and close the glottis. Shufeldt’s descriptions, for example, apparently intermingle the 2 muscles of the larynx. None describes the constrictor muscle properly. Knowledge of the morphology of the larynx and of the muscles operating it is essential before the mechanism of this structure during respiration and feeding can be understood. Moreover, opening and closing of the glottis may play a role during calling and singing of birds by regulating the rate of air flow through the trachea. Questions such as the speed of opening or closing of the glottis may be critical in elucidating the production of avian sounds.

MATERIALS AND METHODS

Dissections were made on 6 adult specimens of Corvus brachyrhynchos from the avian anatomical collection of the American Museum of Natural History or which were collected especially for this study. The specimens were prepared routinely for gross dissection, i.e., fixed in 10% formalin and stored in 60–70% alcohol. All dissections were done with the aid of a Wild M5 stereo dissecting microscope; I used an iodine solution to stain the muscles. Drawings were made directly from the dissected preparations with the use of a drawing tube (camera lucida) attached to the microscope.

NOMENCLATURE

The names of the several skeletal elements of the larynx and of the associated muscles have been in a state of confusion partly because of the lack
of study of these features and partly because of some variation among different groups of birds. In its attempt to standardize avian anatomical names, the International Committee on Avian Anatomical Nomenclature (ICAAN) has suggested (not yet published) a set of names based largely on work done on the domestic chicken (Gallus gallus). Most, but not all of these names, are reasonable and should be used; my only disagreement lies with the terms recommended for the 2 major laryngeal muscles that open and close the glottis. These and a few other nomenclature problems should be discussed pending publication of the Nomina Anatomica Avium.

The larynx of the Gallus is comprised of 4 bones, the large cricoid, the small dorsal procricoid, and the paired arytenoids. The cricoid possesses a pair of dorsal wings, and each arytenoid has a long caudodorsal process. In Corvus, the wings of the cricoid and the process of the arytenoids are represented by separate skeletal elements which must be designated by distinct terms. I know of none available in the literature and propose to call these structures the dorsal cricoid (homologous to the cricoid wing in Gallus) and the dorsal arytenoid (homologous to the caudodorsal process of the arytenoid in Gallus). The cricoid in Corvus could be referred to as the ventral cricoid and the arytenoid as the ventral arytenoid, but I would oppose such a terminology as unnecessarily cumbersome. Thus the larynx of Corvus is comprised of 3 separate skeletal elements as opposed to 4 in Gallus.

Names for the muscles pose special problems for 2 reasons. The first stems from the fact that 2 muscles of the larynx have not been described earlier, and the second arises as a nomenclatural question of the names of the 2 main laryngeal muscles.

In an earlier study (Bock 1972:73–75), I described a new muscle lying on the dorsal surface of the major laryngeal muscles and associated with the posterior flaps of the larynx. This muscle was named the M. thyreohyoideus superior. One of the goals of this study was to provide a better description of this muscle; however, 2 muscles were found. These muscles control elevation and depression of the posterior flaps. I know of no earlier descriptions of these muscles aside from my earlier tentative description of the one; hence these muscles must be named. They appear to be part of the M. cricothyreoideus system so that appropriate names would be the M. cricothyreoideus superior (= M. thyreohyoideus superior of Bock 1972) and the M. cricothyreoideus posterior. Many workers have pointed out that birds do not possess a thyroid cartilage, making the name M. thyreohyoideus inappropriate for an avian muscle (e.g. George and Berger 1966:262). A substitute name, the M. cricothyreoideus, has been proposed by the ICAAN for the M. thyreohyoideus and I will use it for these parts of this muscle system.

The structure of the M. ch. superior and M. ch. posterior in Corvus does
not provide strong clues to their evolutionary origin and possible homology. Fortunately dissection of the larynx of the Rock Dove (*Columba livia*) demonstrated clearly that these muscles are derivatives of the M. cricothyroides system. In this species, the M. ch. superior arises from the posterior flap of the larynx but inserts on the basihyale with the rest of the M. cricothyroides (pers. obs.). Dissection of *Plectorhyncha* (Meliphagidae) revealed a condition of the M. cricothyroides superior that is intermediate to those seen in *Columba* and in *Corvus*. About half of this muscle in *Plectorhyncha* arises from the hyoid skeleton, mainly from the ceratobranchial, and the rest from the dorsal edge of the cricoid cartilage (pers. obs.).

The names for the dilator and constrictor muscles of the glottis pose a greater problem. These muscles have been called the M. thyroarytenoideus and M. constrictor glottidis by most workers (George and Berger 1966:264), but these names are not the best possible. An alternate set of names, the M. laryngeus superficialis and the M. laryngeus profundus, has been suggested by the compilers of the *Nomina Anatomica Avium*. I prefer not to use these names because they necessitate 2 changes where only 1 is necessary, because they provide only a vague indication as to the position of the muscles, and because they could lead to possible confusion with other laryngeal muscles. The M. cricothyroides superior lies superficial to the M. laryngeus superficialis, and the M. l. profundus could be interpreted as a muscle lying on the ventral surface of the larynx and hence confused with the main part of the M. cricothyroides. I propose the names M. dilator glottidis (= M. thyroarytenoideus, M. laryngeus superficialis) and M. constrictor glottidis (= M. laryngeus profundus) for these muscles because these names are descriptive of the major functions of the 2 muscles and because this set of names necessitates only 1 name change from those used by most avian anatomists (e.g., George and Berger 1966). The M. dilator glottidis is similar to the names used for this muscle by Gadow (1891:718) and by Edgeworth (1935:176).

**Description**

*The larynx.*—The larynx, when viewed from the oral cavity, is a low mound lying in the floor of the pharynx just posterior to the base of the corneous tongue and immediately anterior to the opening of the esophagus (Fig. 1). The laryngeal mound is covered with a number of posteriorly projecting papillae and terminates in a pair of posterior flaps. The flaps are comprised of a row (sometimes 2 rows) of larger papillae and delimit the anterior end of the esophagus. In many birds, these flaps are distinct projections of the laryngeal mound and are much larger than those present in *Corvus*. The glottis, or opening of the trachea, lies between and just anterior to the paired
laryngeal mounds. The floor of the glottis has a pair of shallow depressions into which fit the anterior ends of the laryngeal mounds when the glottis is closed completely. A narrow sulcus or groove separates the posterior halves of the 2 mounds; it begins at the level of the pointer in Fig. 1A. The floor of the sulcus is formed by the M. constrictor glottidis.

*Laryngeal skeleton.*—A complex of 8 skeletal elements (cartilage, partly ossified, or completely ossified) constitutes the skeleton of the larynx (Fig. 2). The main bone is the cricoid, which forms the ventral floor and lateral walls of the larynx and supports the other bones. The tracheal rings attach to the posterior edge of the cricoid. One or more tracheal rings may be partly or completely fused with the cricoid in some birds. The cricoid is a trough-like structure, narrowest and lowest at its anterior end. Its sides slope gradually dorsally to reach their maximum height at their posterior end. Articular surfaces for the dorsal cricoids are present on the dorsal rim of the cricoid walls just anterior to their posterior corners.

Fig. 1. External view of the larynx of *Corvus.* (A) Dorsal view. (B) Lateral view. Abbr: G—glottis; LM—laryngeal mound; PLF—posterior laryngeal flap; S—sulcus.
Fig. 2. Laryngeal skeleton of *Corvus*. (A) Dorsal view. (B) Ventral view. (C) Lateral view. (D) Medial view. (E) Ventral view of the main dorsal complex of bones (the dorsal arytenoid is omitted). Abbr: A—arytenoid; C—cricoid; DA—dorsal arytenoid; DC—dorsal cricoid; PC—procricoid; TR—tracheal ring.

The cricoid forms the foundation for the larynx and provides the support for the other laryngeal bones and for the laryngeal muscles. In addition 3 pairs of extrinsic muscles take origin from or insert onto its outer ventral and lateral surfaces: these are the M. cricothyoideus, the M. tracheothyoideus (not in all birds) and the M. tracheolateralis. (The description by Gaunt and Gaunt [1977:5] that the M. tracheolateralis of *Gallus* “extends from the glottis caudad along the lateral margins of the trachea” is a terminological slip. They meant to say that this muscle attaches to the larynx or to the cricoid, not to the glottis.) These muscles are parts of the tongue and/or respiratory-vocal systems. The remaining 7 bones of the laryngeal skeleton constitute the movable elements that support and alter the position of the glottal lips.

The paired dorsal cricoid bones articulate with the dorsal rim of the cricoid
close to its posterior corner. These bones curve posterodorsally and then somewhat ventrally just before their articulation with the lateroposterior surfaces of the procricoid. The 2 dorsal cricoids approach one another at the midline but do not meet. The procricoid is a cuboidal structure lying in the dorsal midline of the larynx. It usually lies at or slightly above the level of the dorsal edge of the cricoid. The procricoid has 4 articular surfaces, 2 at its lateroposterior corners for the paired dorsal cricoids and 2 at its lateroanterior corners for the paired arytenoids. The paired arytenoids extend anteriorly from the procricoid, first at the same level and then curving ventrally to approach the floor of the cricoid. Their free anterior ends are generally curved slightly laterally, usually more than shown in the illustrated specimen. (The free tips of the arytenoids in this specimen may have been eroded away during preparation.) An articular surface lies on the dorsal surface of the arytenoid midway between its anterior and posterior ends; the rod-like dorsal arytenoid articulates at this point. The 2 arytenoids support the glottal lips, while the dorsal arytenoids form the edges of the sulcus.

Movement of the entire dorsal complex relative to the cricoid is permitted by the articulations between it and the paired dorsal cricoids. The arytenoids can swing lateromedially as well as ventrodorsally about their articulations with the procricoid, and the dorsal arytenoids are free to move relative to the arytenoids. Opening and closing of the glottis is accomplished largely by movement of the arytenoids relative to the procricoid, but some movement of the dorsal cricoids and of the procricoid probably also contributes to glottal action.

Laryngeal muscles.—Four sets of intrinsic muscles are found in the Corvus larynx. 2 operating the posterior flaps and 2 controlling the opening of the glottis. The extrinsic muscles attaching to the larynx will not be considered herein; these are usually considered part of the tongue apparatus and/or of the respiratory-vocal system.

M. cricothyroides superior: The origin of the M. ch. superior is from the dorsal rim of the cricoid (Fig. 3) just at the point where the rim slopes ventrally. The fibers of the M. ch. superior originate contiguously with the dorsal head of origin of the M. cricothyroides (=M. thyreothyroides); separation of these 2 origins must be done with care. Insertion of this muscle is into the mucosa underlying the large papillae of the posterior flap. The M. ch. superior is a thin, parallel-fibered muscle overlying the posterolateral corner of the M. dilator glottidis. The fibers are 5–6 mm long and the muscle cross-sectional area is about 0.2 mm² (2 mm wide and about 0.1 mm thick). The M. ch. superior elevates the posterior flap.

The M. ch. superior is a very thin muscle closely associated with the mucosa
covering the laryngeal mound. It is easily destroyed when removing the epithelium and mucosa in preparation to dissect the main laryngeal muscles and hence has escaped the notice of morphologists. Moreover, this muscle is so closely appressed to the surface of the M. dilator glottidis that it would escape detection in histological sections, especially as the fibers of the two muscles run in the same direction. Its discovery in *Ciridops* (Bock 1972) was by good fortune because the epithelium covering the larynx peeled away easily without damage to the muscle.

M. cricothyoideus posterior: The origin of the M. ch. posterior is from the dorsal rim of the cricoid at its dorsoposterior corner (Fig. 3). The muscle is a thin band that runs along the ventral edge of the posterior flaps from one side of the cricoid to the other. Possibly the fibers from the right and left sides of the larynx meet in a medial raphe, but no sign of a midsagittal connective tissue line could be seen. The parallel fibers of the M. ch. posterior are about 10–12 mm long (from one origin to the other) and form a thin band with a cross-sectional area of 0.1–0.2 mm² (width 1 mm and thickness 0.1 to 0.2 mm). The muscle acts like a sphincter and serves to depress the posterior flaps.

The M. ch. posterior is buried within the mucosa forming the ventral half of the posterior flaps and is easily destroyed when removing the epithelium and connective tissue to expose the muscles. Its discovery was the result of a search for a muscle antagonistic to the M. ch. superior.

M. dilator glottidis: The M. d. glottidis is the superficial glottal muscle and almost completely obscures the M. constrictor glottidis (Figs. 3, 4, and 6). It originates from the posterior and dorsal surfaces of the dorsal cricoid (Fig. 6); none of the fibers originate from the cricoid in *Corvus*. Note that in some other birds, e.g. *Gallus* and *Columba*, in which a distinct cricoid does not exist, the M. d. glottidis arises from the cricoid, that is, from the dorsal wing of the cricoid. Its description in *Ciridops* (Bock 1972) is not quite correct as it most likely does not originate from the cricoid cartilage. Insertion of the M. d. glottidis is along the laterodorsal surface of the anterior end of the arytenoid (up to its articulation with the dorsal arytenoid) and along the lateroventral surface of the anterior ½ of the dorsal arytenoid. Most of the fibers originate from the posterior surface of the dorsal cricoid and curve around the dorsal surface of that bone before extending to their insertion. The M. d. glottidis is parallel-fibered with the fibers varying in length from 3–9 mm (lateral-most) to 3–4 mm (medial-most). The cross-sectional area is about 3 mm² (width is 4 mm and thickness is 0.5 to 1 mm with an average of 0.75 mm).

Upon contraction, the M. d. glottidis rotates the arytenoid laterally about its articulation with the procricoid as well as elevating it. Moreover, the
Fig. 3. Superficial muscles of the larynx of *Corvus*, showing the muscles regulating the posterior flap. (A) Dorsal view. (B) Lateral view. Abbr: M ch p—M. crico-hyoideus posterior; M ch s—M. crico-hyoideus superior; M c g—M. constrictor glottidis; M d g—M. dilator glottidis; PLF—posterior laryngeal flap.

dorsal cricoid would be rotated about its longitudinal axis, i.e., the bone rotates about its articulations with the cricoid and the procricoid. Because of the shape of the dorsal cricoids, this longitudinal rotation would raise the posterior ends of the bones and hence elevate the procricoid and with it, the paired arytenoids. Thus the entire dorsal complex of bones and the lips of the glottis are elevated with respect to the cricoid. This action increases the maximum possible opening of the glottis.

M. constrictor glottidis: The M. c. glottidis lies deep to the M. d. glottis (Figs. 3, 4, 5, and 6) and is a much more complex muscle with respect to its origins and insertions. For clarity of description the muscle will be divided into 3 parts: A, B, and C, but these subdivisions merge into one another without any sign of a break. These parts were not distinguished in *Ciridops* (Bock 1972) as the muscle was incompletely described.
Fig. 4. Main laryngeal muscles of *Corvus*. (A) Dorsal view with the M. dilator glottidis removed from the left side. (B) Ventral view with most of the cricoid and much of the right M. constrictor glottidis removed. Abbr: M c g—M. constrictor glottidis; M d g—M. dilator glottidis.

The origin of the M. c. glottidis is from a midsagittal raphe dorsal and anterior to the procricoid and the adjacent arytenoid (parts A and C), and from the lateral surface of the arytenoid anterior to its articulation with the dorsal arytenoid (part B). Fibers run laterally and anteriorly to several areas of insertion; these will be described separately. Part A inserts along a thin line along the medial surface of the cricoid just below its dorsal rim and along the medial surface of the dorsal cricoid. Fibers of part A vary from 9 mm long (anterior fibers) to 2–3 mm long (posterior fibers); this part is 7 mm wide and 0.25 to 0.5 mm thick for a cross-sectional area of about 2–3 mm². Part B inserts on the floor of the cricoid anterior to the opening of the glottis, but at least half of the fibers are continuous with
Fig. 5. The M. constrictor glottidis of *Corvus* seen in dorsal view. (A) Overview of the muscle with a portion of part A removed on the right side. (B) Deeper and more detailed view showing parts B and C and the areas of insertion. See text for a more detailed description of this muscle.

Those of the contralateral muscle, forming a ring-like sphincter about the anterior ends of the paired arytenoids. The parallel fibers of part B are 8–9 mm long and form a band 1.0 mm wide and 1.0 mm thick, which results in a cross-sectional area of 1.0 mm². Part C inserts onto most of the mediadorsal surface of the arytenoid between its articulations with the procricoid and the dorsal arytenoids and onto the ventral surface of the dorsal arytenoid for a short distance posterior to its articulation with the arytenoid. This part is fan-shaped in appearance, but its fibers are essentially parallel. The fibers are only 2–5 mm long (from posterior to anterior) and are 3 mm wide and 1 mm thick giving a cross-sectional area of 3 mm².
Fig. 6. Main laryngeal muscles of Corvus seen in posterior view. The origin of the M. dilator glottidis (M dg) from the posterior surface of the dorsal cricoid and the sphincter like structure of part B of the M. constrictor glottidis (Mcg) are emphasized.

Because of its complex fiber arrangement, the action of the M. c. glottidis to close the glottis is more complicated than the opening by the M. d. glottidis. Contraction of part C serves to draw the 2 arytenoids toward the midline in a simple closing action. However because this muscle part lies close to the articulation of the arytenoid with the procricoid, its moment arm is short and hence its torque development is relatively low. Part B acts like a simple sphincter muscle to draw the tips of the arytenoids toward the midline. Moreover, it draws the tips of the arytenoids to the floor of the cricoid because of the insertion of approximately half of the fibers to the cricoid cartilage anterior to the opening of the glottis. It is the combined action of parts B and C that closes the glottis and depresses the tips of the glottal lips. Part A has no role in closing the glottis. Rather, contraction of this part serves to lower the entire dorsal complex of bones relative to the cricoid, an action that is antagonistic to the elevating action of the M. d. glottidis.

The operation of the 2 glottal muscles is thus (a) to open and elevate the glottal lips and (b) to close and depress them, and the arrangements of fibers in the 2 muscles permit full antagonistic actions.

DISCUSSION

A comparison of the description of the skeletomuscular system of the Corvus larynx with those presented earlier suggests that the passerine larynx had never been described properly and that the glottal muscles in birds had
never been described correctly. (This includes the description of Bock 1972, which can, however, be corrected in light of the redescription of the glottal muscles presented above.) Indeed from an examination of the text and figures of earlier descriptions of these muscles, it is not possible to understand how these muscles, especially the M. constrictor glottidis, operate. A description of part C has never been presented clearly; the descriptions of Gadow (1891:817) Edgeworth (1935:176), and White (1965:1894) are suggestive at best. Shufeldt (1890) shows most of the laryngeal bones (the dorsal arytenoids are lacking) but his indications of the attachments of the muscles as well as his text description and figure of the M. d. glottidis (= his thyreoarytenoideus, Fig. 18, p. 46) are confusing. The description of the glottal muscles by Fisher and Goodman (1955:36), which is followed by George and Berger (1966:264), does not appear to be correct (although I have not been able to check it by dissections on *Grus*), but more importantly it is impossible to see how the M. c. glottidis can close the glottis.

The more complex system of bones in the *Corvus* larynx as compared to that of *Gallus* and *Columba* raises several interesting questions. The first is what is the arrangement of laryngeal bones in the different orders of birds? Next is whether the morphology of the M. dilator glottidis and M. constrictor glottidis alters with change in the laryngeal skeleton. Most interesting is the mechanism of evolutionary change whereby the cricoid wing separated from the body of the cricoid and became a distinct bone with a diarthrosis between it and the cricoid: a similar question can be asked about the evolution of the dorsal arytenoid. And lastly is the question of whether the evolution of the more complex larynx in *Corvus* and presumably other passerine birds is associated with the evolution of the most complex syringeal muscles and more complex song in these birds.

The cross-sectional areas (and presumed force developments) of these muscles are larger than expected if these muscles simply opened and closed the glottis during respiration. An explanation may lie in one or a combination of possible glottal actions. The first is that the glottis may have to be opened and closed very rapidly: rapid movement requires high acceleration which necessitates large force development. Second is that the glottis may have to be opened and closed many times in rapid succession over a period of time. Or it may be necessary to hold the glottis fully opened or tightly closed against some resistance for a long period of time. Both actions would require a muscle with a large cross-sectional area to provide enough fibers to permit recruitment of fresh fibers as the contracting fibers become fatigued. A subsequent question would be the possible functions of such muscle actions in the role of the glottis in respiration, swallowing, or sound production.
Although movement of the glottal lips is a simple scissorlike opening and closing, the morphology of the underlying skeletomuscular system proved to be more complex than expected. Comprehension of the mechanics of glottal action is not possible without a detailed knowledge of the structure of the laryngeal skeleton and muscles. In closing, I would like to emphasize the need and importance of thorough, careful dissection and description as the foundation of avian morphology and all other studies, e.g. functional and evolutionary analyses, based upon it.

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HABITAT USE BY YELLOW-RUMPED WARBLERS AT THE NORTHERN EXTREMITIES OF THEIR WINTER RANGE

KENNETH J. WILZ AND VINCENT GIAMPA

The Presque Isle peninsula, a state park adjacent to the city of Erie, Erie County, Pennsylvania (42°10'N, 80°05'W), has long been known for its unusual floral and faunal characteristics. This narrow peninsula jutting 11.3 km into Lake Erie offers a great diversity of environments (from sandy beaches to climax forests) in a compact space. Many species of migrating birds visit the area, and one is struck also by the richness and unusual nature of the breeding and wintering bird communities (Stull 1965). One unusual feature is the presence of a large population of wintering Yellow-rumped Warblers (Dendroica coronata) (See Christmas Counts, Am. Birds, 1957–1977). Numbers reported on Christmas Counts have ranged from 19 (1957) to 297 (1975) and seem to be increasing.

A careful survey of the Christmas Count data underlines the unusual nature of this large population. There is no other area in the Great Lakes region, at least amongst those covered by Christmas Counts, where Yellow-rumped Warblers occur in anything like these numbers. Counts in adjacent areas have yielded no or only a few birds. One has to drop as far south as Tennessee–North Carolina to obtain comparable numbers. Relatively large populations can be found along the Atlantic coast to Massachusetts during mid-winter. However, this can be explained by the warming effects of the Gulf Stream, as well as possibly other factors.

Why do these birds overwinter so far north? The Yellow-rumped Warbler is unusual among Parulids in that it is much more of a generalist feeder. Although 73% of its food for the year is animal matter, it also can subsist on various fruits (Palmer and Fowler 1975). Northern bayberry (Myrica) has been reported (Hausman 1927) in the diet of Yellow-rumped Warblers and is common on Presque Isle. However, no one has collected regular data over a period of time to link the warblers to this food source and/or to others. We here describe results of a study designed to provide an explanation for this unusual population.

METHODS

Data were collected from 16 January to 18 March 1975 and 13 November 1975 to 8 March 1976. Over 230 hours of observation were accumulated (the majority by Giampa); the peninsula was visited approximately every other day.

Field tactics differed between the seasons. During the first season our approach was
to maximize the time spent in observing the warblers. This meant concentrating on the eastern quarter of the peninsula, since Christmas Count observations and other reports (J. Stull and D. Snyder, pers. comm.) had suggested that the birds were confined mainly to this sector. Within this sector most areas were sampled on a given visit. However, once contact was made the birds were observed sometimes for 30 min or more. Every effort was made to minimize disturbing the birds. Binoculars were used to observe birds and field notes were either written or tape recorded. All aspects of behavior were recorded, including location, number, foods taken, rate of movement, interspecific relations, predation, etc., as well as appropriate weather data. Data were collected during all day-light hours.

During the second season, when the bulk of the data reported here were collected, efforts concentrated on 2 smaller areas in the eastern portion. The first of these, the pine plot or transect, was chosen since it had yielded regular, consistently high counts the previous winter. It seems typical of a stretch of pine-dominated (*Pinus rigida*) habitat that extends to the middle of the northern side of the peninsula. These pines are 15–18 m in height, and the stand averages 95 m wide, with a trail in the middle. The understory is dominated by scattered patches of bayberry averaging 1 m in height. The second area, the cottonwood plot or transect, was directly east of the pines (beginning 230 m from beach house 10); it had yielded irregular, but sometimes high counts the previous winter. This area contains no pine; the canopy is cottonwood (*Populus deltoides*), spaced at intervals of approximately 3.5 m and with heights of 4.5–18 m. The undergrowth contains by far the highest density of bayberry on the peninsula, estimated to be at least 300–400 plants/ha, ranging from .9–3+ m in height. Both areas are subject to little human interference in winter and contain no artificial feeding stations. (For further information on the geography and botany of Presque Isle, see Jennings 1909 and Kormondy 1969.)

Within each study area a transect line was established (Emlen 1971, Grubb 1975). They ran through the center, with uniform vegetation along the line as well as on both sides. Each line consisted of 10 45.7 m units, which were sampled 3 times/week (except for 4 in week 1, and 2 in weeks 5 and 6), for a total of 44. Observations started 1 h after sunrise, and the area in which observations began was alternated. At the end all relevant weather data were gathered.

In sampling, the observer(s) walked both directions along the transect line and recorded the number of birds, their transect unit, and other species present (excluding waterfowl). Within a unit, birds judged to be part of an intraspecific flock (Morse 1970) were recorded as such. Side boundaries were set at 45.7 m in each direction. The observations lasted 50.8 ± 12.1 min/transect (n = 88). Two observers were used on many counts, but there is no evidence that the second observer significantly affected the scores, except in improving the accuracy of the numbers estimated. In moving from 1 transect unit to the next, birds were not recorded again if they had been “pushed” by the observer(s), or if they had moved spontaneously. By collecting data in passing back through the transect, we recognize that some “double counting” occurred. For many purposes this is of no real consequence since we were interested in relative scores. Also, the birds' rate of movement was great enough that the amount of double counting is not especially high. Finally, we wanted to collect as much information per trip as possible; by disregarding events on the return, much information would have been lost.

Attempts were made to accurately assess food choice in the transect areas. Our method consisted of point observations (Morse 1972). The observer moved slowly within the study area, located a bird, and recorded its first foraging act (actual use of mouth-
parts in pecking at materials). Another individual was then located and recorded; no individual was knowingly recorded more than once. Both habitats were open enough that individuals were located with close to randomness. In most cases 2 observers were used in sampling, and the results were compared to assure that the data were representative. Some feeding data were collected on other species, with particular attention given to those competing for the same resources.

In the cottonwood area bayberry counts were conducted at the end of each week. Ten circular sampling areas were established along the transect line; these had a diameter of 30.5 m and were spaced at 45.7 m intervals. Nine plants were sampled each week. These were chosen using a random numbers generator which identified sampling area, distance from a reference point in the center, and compass direction. Once the plant was selected the berries available to the birds on the plant and on the ground were counted. Counts of ground berries included a .093 m² area at the base of the plant. Estimates of bayberry numbers in the pine area were also made weekly.

RESULTS

For the season the Yellow-rumped Warbler was found to be the predominant species in both habitats. We saw 28 species (excluding waterfowl) in the pine plot, but of all birds sighted on the outward and backward censuses 51.5% were Yellow-rumped Warblers, an average of 56.8 birds per census. Similarly, 25 species were detected in the cottonwood sector, but 55.7% were Yellow-rumped Warblers, an average of 48.5 per census. However, there were dramatic fluctuations in numbers over the season, especially in the cottonwood area, and also major differences between the plots. This is shown in Figure 1 which illustrates the relative weekly means for both transects for the entire season. The graph shows that the numbers in the pine area remained reasonably stable, though at a somewhat higher level during mid-winter (December 14–February 14). But in the cottonwoods the warblers were seen in low numbers or not at all except for a period of nearly 5 weeks in the latter part of mid-winter, when there was a dramatic influx. The lower numbers in the cottonwood as compared to the pine plot during early winter (November 23–December 13) and late winter (February 15–March 6) are significant (p < .02, Mann-Whitney 2-tailed test. Siegel 1956).

The very large influx of Yellow-rumped Warblers into the cottonwood-bayberry area coincided with heavy snow that accumulated during most of January and early February. Snow cover seemed to be a major variable affecting habitat choice. A comparison of the number of birds in the cottonwoods during mid-winter on days of partial or no snow cover with days of complete ground cover yields strikingly different means: 7.7 and 31.2 respectively (n = 8 and 14). This difference is significant at the .02 level (Mann-Whitney 2-tailed test). Temperature and wind, in contrast, could not be established as factors which significantly influenced habitat choice, though wind did seem to influence the height at which the birds foraged in the
Fig. 1. Fluctuation in estimated numbers of Yellow-rumped Warblers over the season for both transect areas (weeks running consecutively starting week of November 23 [November 23–March 6]).

more exposed cottonwood habitat. (The mean temperature for the winter of 1975–76 was .9°C, with early winter at 5.6°C, mid-winter at −2.7°C, and late winter at 2.3°C. Wind along the lake was substantially greater than inland, an average of 16.2 knots in January, 1975 and 13.4 knots in February, 1975 as compared to 10.2 and 9.7 for the same periods at Youngstown, Ohio [data courtesy of U.S. Department of Commerce and U.S. Coast Guard].)

During the period of heavy snow cover, data were collected on the feeding behavior of the Yellow-rumps in the cottonwood area. Of 254 independent observations over a period of days, 89% of foraging was on bayberry fruit. These results are consistent with those collected the previous year where individual birds were followed for a period of time. Figure 2 shows the 3-week means of warblers plotted against the 3-week means of bayberries per plant over the season in the cottonwood area. The numbers of warblers foraging on the bayberries do not correlate with the berries available. However, the graph does indicate that a low number of (available) bayberries can support a large population of Yellow-rumped Warblers.

In the pine area the feeding choice of the warbler was much more diversified. A single flock sometimes included individuals clinging to the bark of pines, picking at pine needles, fluttering on the tree trunks, eating bayberries from bushes, and moving about on the ground. Of 195 sample
Seasonal numbers of Yellow-rumped Warblers in relation to the number of bayberries available/plant (November 23–March 6).

Feeding observations (middle February of 1975, ground open, mild temperature) 56% were of birds in pines, 37% were in bayberry bushes or on the adjacent ground (where it was assumed that bayberry fruit was the primary food), almost 6% were of birds in deciduous trees, with 1% in the "other" category. Of the pine feeding about 45% was within 3 m of the ground along the main trunk. In the pine area by mid- to late winter the supply of bayberries on the plants was very low. Ground feeding seemed to be more important then. On 21 and 27 February 1976 of 6 flocks of 10 or more located in the pines to the west of the study area, 4 were observed to be feeding wholly on the ground for the duration of observation.

The flexibility of the warbler's feeding tactics was also illustrated by the fact that they were observed feeding at fallen, partly decayed logs and feeding on spider eggs while hovering under the eaves of a beach house. This latter activity was observed only once, during heavy snow cover. We noted no active invertebrates in either season during the mid-winter period.

There seemed to be only 2 other sites where the warblers could be located with regularity. One was an extension (westward) of the pine transect. The other was to the south in the immediate area of Beach 11, where there was a small amount of pine and bayberry. At no time were birds seen feeding outside the range of the bayberry plant during mid-winter. Our estimate of total birds on the peninsula for the winter of 1975–76 is 500, somewhat higher than the 20 December 1975 Christmas Count.
Of the 4635 Yellow-rumped Warbler observations along both transects, 93.1% were flocking with 1 or more Yellow-rumped Warblers, with an average flock size of 9.6 ± 1.3. The rate of movement of a foraging flock was brisk and almost constant. Some flocks appeared quite cohesive, though flocks were often loosely organized, with individuals and/or small groups joining or leaving. Agonistic behavior was almost completely absent during mid-winter, though it occurred some in early spring. Also, as spring approached flocks seemed to become less stable, resulting in a more dispersed population.

The warblers commonly were part of larger interspecific associations. At the beginning of the season loose flocks were composed of many species, but by the middle of winter they were reduced to a nucleus of Yellow-rumped Warblers, Black-capped Chickadees (Parus atricapillus), and Downy Woodpeckers (Picoides pubescens). Quantitative analyses of these interspecific associations, based on the transect unit in which birds were located, show that these flocks were formed with equal regularity in both habitats. Downy Woodpeckers consistently were "absolute followers" (Morse 1970) within these flocks; there were about as many unambiguous cases of warbler following chickadee as vice versa. As with Yellow-rump social interactions, no instances of direct competition for food during mid-winter were noted. This was the case despite the fact that the feeding habits of the chickadees seemed quite similar to that of the warblers. In addition to warblers and chickadees, Common Flickers (Colaptes auratus), Downy Woodpeckers, Starlings (Sturnus vulgaris), and Tree Sparrows (Spizella arborea) fed on bayberry fruit with some regularity.

Six predatory bird species were recorded during each season. Of these the American Kestrel (Falco sparverius) and Northern Shrike (Lanius excubitor) were seen regularly, with 3 instances each of active pursuit of the warblers during the second season alone. Of these all but one took place in the more open cottonwood area.

DISCUSSION

A large population of Yellow-rumped Warblers remains throughout the winter in the eastern portion of Presque Isle near Erie, Pennsylvania. Such a population is remarkable considering the latitude and the wind chill factor. Probably the most important factor in allowing its presence is the large amount of bayberry. The local distribution of the warblers matches that of the bayberry. Also, during times of heavy snow cover and low temperatures, large numbers of warblers can be found in the area of the highest bayberry density where the warblers concentrated almost totally on bayberry fruit for food. For the bayberry to be used as almost the exclusive food during in-
clement weather, it must be of high nutritional value to support the warbler's high metabolic rate (Emlen 1966). Hausman (1927) reports that the waxy substance on the bayberry is a fat composed of glycerides of steric, palmitic, myristic, and oleic acids. Also, the berry contains traces of protein and carbohydrate.

Apparently heavy snow, by eliminating feeding on the ground and at the base of trees and shrubs, makes the cottonwood-bayberry area the most efficient one in which to forage. Without snow, even when bayberries were abundant, this area was little used. Gottfried and Franks (1975) reported substantial shifts in feeding locale of Dark-eyed Juncos (Junco hyemalis) with varying weather conditions, especially snow cover (see also Morse 1970, Heppleston 1971, Grubb 1975). Heavy snow occurred fairly late in the season when the invertebrate supply was likely depleted by earlier foraging activity (see Gibb 1960). It is possible that similar weather conditions earlier in the winter would not have produced the same shift.

Feeding away from the cottonwood area (mainly in the pines) has several advantages. One is a greater protection from predators. Indeed, the constant movement and lack of a small home range may in itself serve as a defensive mechanism (e.g., Gibb 1960). A greater protection from the wind is also important (Gottfried and Franks 1975). Also, in the pines feeding behavior was very diversified. Thus, it is probable that a greater variety of foods was taken, allowing for better nutritional balance. Morse (1970, 1971) has referred to the foraging plasticity in this species.

During both seasons the bayberry numbers on the branches were very low by early February even in the best areas. Probably a good proportion of this loss can be attributed to the "harvesting" by birds. There appears to be a small margin of error, at least so far as bayberry as a food resource is concerned. Gibb (1954, 1960) also reported a substantial decline in food availability by late winter. Pulliam and Enders (1971) reported it probable that 75% or more of the total seed crop was eaten by finch species in central North Carolina during a typical winter. West (1967), on the other hand, found that a much smaller proportion of available food was required by wintering Tree Sparrows in Illinois.

The benefit of interspecific flocking has been the subject of much attention (Wilson 1975). In our case protection from predators would appear to be an important biological advantage, since much foraging must be done in the open. Siegfried and Underhill (1975) have recently shown experimentally the importance of numbers in detecting predators. Several authors (Morse 1970, Austin and Smith 1972, Kricher 1975) report that members of the genus Parus form the nucleus to which other species are drawn. This was not the case in our study: chickadees often were seen following the warblers.
A possible reason for this is the dominance in numbers of the warblers. Our data are also at variance with reports of substantial fighting amongst individuals of a flock, and the resulting partitioning of food niches (Morse 1967, 1972). Our data agree more with that of Pulliam and Enders (1971) who found substantial overlap in food use among finch species and Austin and Smith (1972) who found very low levels of aggression in flocks of wintering birds in southern Arizona.

SUMMARY

The Yellow-rumped Warbler (Dendroica coronata) is a common winter resident on Presque Isle, a peninsula jutting into Lake Erie, Pennsylvania. This population was studied during the winters of 1974–75 and 1975–76 with the intent of exposing the factors which enable the warblers to remain this far north. Foraging behavior was found to be highly diversified and habitat selection was strongly influenced by weather variables and food accessibility. Bayberry was found to be the major food resource during periods of inclement weather. Though numbers fluctuated greatly in the study areas, the warblers remained on the peninsula throughout the winter. They were normally in flocks, which regularly included several other species.

ACKNOWLEDGMENTS

We wish to thank the staff of Presque Isle State Park for their cooperation and Edinboro State College for supplying transport for at least some of the trips. We also wish to thank Dr. D. Snyder and Ms. J. Stull for their advice in the initial stages of the project. Finally, we wish to thank Mr. S. Nodler and a number of other Edinboro students who accompanied V. Giampa during many of the first-year visits.

LITERATURE CITED


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HABITAT SHIFT AND ROADSIDE MORTALITY OF
SCARLET TANAGERS DURING A COLD WET
NEW ENGLAND SPRING

DAVID C. ZUMETA AND RICHARD T. HOLMES

For insectivorous birds breeding at temperate or higher latitudes, the
timing of arrival in spring is crucial. A primary hazard is to arrive too early
when suitable food sources are lacking or when the birds would be subject
to the effects of unsettled weather. Swifts, flycatchers, swallows, warblers,
and tanagers appear to be especially vulnerable to extended periods of cold
or rainy weather when they first arrive in the north (Forbush 1904, Bagg
and Eliot 1937, Manville 1957). Scarlet Tanagers (Piranga olivacea),
generally arboreal, have been recorded feeding on or near the ground during
inclement weather (Hancock 1838, Eaton 1914, Bent 1958, Wetmore 1964,
Bull 1974), often in habitats that differ from those typically occupied by
the species (Nichols 1956, Manville 1957).

Such an event occurred in New England during a wet, cool period in late
May 1974 when many insectivorous birds, but especially Scarlet Tanagers,
shifted from their normal forest habitats to open areas where they engaged
in extensive ground feeding. Some species, again primarily tanagers, suffered
high mortality. This event has been described briefly by Kane and Buckley
(1971), Kent (1974), and Finch (1975a). However, these authors presented
little quantitative data on the magnitude of this phenomenon or its potential
impact on breeding populations. In this paper, we describe the change in
habitat and roadside mortality of Scarlet Tanagers and certain other insect-
vorous birds during spring 1974 in north-central New England, relate the
phenomenon to decreased insect availability in forests caused by wet, cold
weather, and consider its possible effect on tanger breeding populations.

METHODS

During spring 1974 we travelled frequently on the roads along the east-central border
of Vermont and in west-central New Hampshire, mainly between the Hanover, N.H.-
 Norwich, Vt. area and the Hubbard Brook Experimental Forest, West Thornton, N.H.
(Fig. 1).

From 26 May, when tanagers and other birds first began appearing along the roadsides,
to 1 June, we made 41 surveys of the number of live and dead birds along segments of
2 Interstate and 8 secondary highways (Fig. 1). The surveys lasted from 5 to 40 min,
each covering 4 to 27 km of roadway. Although some highway stretches were surveyed
only once, other routes were travelled on several consecutive days. For each count, data
were recorded on the times, distances, speed and direction of travel, on weather condi-
Fig. 1. Major area of occurrence (hatched in inset) of grounded tanagers and other birds along east border of central Vermont and in west central New Hampshire, 26 May–1 June 1974. Dark lines represent roadside survey routes. • = locations where weather records were obtained. Scale: 10 cm = 52 km.
RESULTS

The phenomenon.—Scarlet Tanagers breed in deciduous and mixed forest throughout the northeastern United States and southeastern Canada. In central New Hampshire, they first arrive between 6 and 12 May, with the bulk of migrants usually appearing between 18 and 25 May (Holmes pers. observ.). In 1974, tanagers were first sighted in central New Hampshire on 9 May (Kent 1974) following the first small wave of migrant songbirds through eastern New England. The first significant migratory movement occurred on 14 May, followed by an extensive, unusually heavy migration between 16 and 18 May, and then a third substantial wave between 24 and 26 May. There was widespread agreement among observers in Rhode Island, Massachusetts, New Hampshire, and Maine that the spring songbird migration through these states was the heaviest in a decade or more (Finch 1975a). Many observers in Vermont and eastern New York reported that Scarlet Tanagers in particular appeared in greater numbers than usual (Kane and Buckley 1974).

On the morning of 26 May in parts of eastern Vermont and west-central New Hampshire tanagers and other birds left their normal forest and woodland habitats and began to appear on lawns, fields, and along roadsides in unprecedented numbers (see Table 1). Many were observed on or along highways on the gravel shoulders, the adjacent mowed grass, or on guardrails.
### TABLE 1

**Occurrence and Mortality of Bird Species Observed Between 26 May and 1 June 1974 Along Interstate and Secondary Highways in North-Central New England**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number Observed on All Highways</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Live</td>
</tr>
<tr>
<td><strong>Mourning Dove, Zenaidura macroura</strong></td>
<td>3</td>
</tr>
<tr>
<td><strong>Chimney Swift, Chaetura pelagica</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>Common Flicker, Colaptes auratus</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>Eastern Kingbird, Tyrannus tyrannus</strong></td>
<td>26</td>
</tr>
<tr>
<td><strong>Eastern Phoebe, Sayornis phoebe</strong></td>
<td>2</td>
</tr>
<tr>
<td><strong>Least Flycatcher, Empidonax minimus</strong></td>
<td>4</td>
</tr>
<tr>
<td><strong>Eastern Wood Pewee, Contopus virens</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>Unident. flycatcher, (Tyrannidae)</strong></td>
<td>7</td>
</tr>
<tr>
<td><strong>Olive-sided Flycatcher, Nuttallornis borealis</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>Barn Swallow, Hirundo rustica</strong></td>
<td>2</td>
</tr>
<tr>
<td><strong>Blue Jay, Cyanocitta cristata</strong></td>
<td>2</td>
</tr>
<tr>
<td><strong>Common Crow, Corvus brachyrhynchos</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>Gray Catbird, Dumetella carolinensis</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>American Robin, Turdus migratorius</strong></td>
<td>48</td>
</tr>
<tr>
<td><strong>Swainson’s Thrush, Catharus ustulata</strong></td>
<td>21</td>
</tr>
<tr>
<td><strong>Unidentified thrush, Catharus sp.</strong></td>
<td>7</td>
</tr>
<tr>
<td><strong>Eastern Bluebird, Sialia sialis</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>Starling, Sturnus vulgaris</strong></td>
<td>73</td>
</tr>
<tr>
<td><strong>Red-Eyed Vireo, Vireo olivaceus</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>Cape May Warbler, Dendroica tigrina</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>Yellow-rumped Warbler, Dendroica coronata</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>Black-throated Green Warbler, Dendroica virens</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>Eastern Meadowlark, Sturnella magna</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>Red-winged Blackbird, Agelaius phoeniceus</strong></td>
<td>13</td>
</tr>
<tr>
<td><strong>Northern Oriole, Icterus galbula</strong></td>
<td>5</td>
</tr>
<tr>
<td><strong>Common Grackle, Quiscalus quiscula</strong></td>
<td>11</td>
</tr>
<tr>
<td><strong>Brown-headed Cowbird, Molothrus ater</strong></td>
<td>21</td>
</tr>
<tr>
<td><strong>Unidentified blackbird, (Icteridae)</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>Scarlet Tanager, Piranga olivacea</strong></td>
<td>225</td>
</tr>
<tr>
<td><strong>Dark-eyed Junco, Junco hyemalis</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>Chipping Sparrow, Spizella passerina</strong></td>
<td>5</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>485</td>
</tr>
<tr>
<td><strong>% Scarlet Tanagers</strong></td>
<td>46.4</td>
</tr>
<tr>
<td><strong>Total birds/hour of travel</strong></td>
<td>44.9</td>
</tr>
<tr>
<td><strong>Total Tanagers/hour of travel</strong></td>
<td>20.8</td>
</tr>
</tbody>
</table>
Tanagers in particular were extremely sluggish, permitting a close approach: many flew with difficulty even over short distances, preferring to hop slowly away.

During the next several days reports came in from Vermont and New Hampshire of flocks of tanagers on the ground and at feeders (Kent 1974, R. Chaffee pers. comm., Holmes pers. observ.), much to the amazement of the general public. Numerous dead tanagers were reported or delivered to the Dartmouth College Museum, the Dartmouth Biology Department, and the local newspapers. Kent (1974) cited cases of tanagers hawking insects over Stinson Lake, N.H., and falling into the water, too weak to return to shore; other tanagers landed on boats in the lake and some were even taken from holding tanks in a local fish hatchery. These birds avidly accepted food when it was offered to them. Other normally arboreal bird species were also displaced to these roadside or lawn habitats (Table 1). All individuals except the tanagers, however, appeared healthy and vigorous, and relatively few were found dead.

**Geographical extent of grounded tanagers.**—From our records and those of Kent (1974) and Finch (1975a), grounded tanagers occurred between 26 and 30 May from southern Maine to eastern Vermont, including most of the northern half of New Hampshire (Fig. 1). Tanagers were reported in greatest frequencies in the 2 major river valleys in the area, the Connecticut and the Pemigewasset-Merrimack.

**Highway surveys.**—Some species observed (Table 1) are typical of roadside habitats (e.g. starlings, cowbirds, robins), but others such as the warblers, vireos, Scarlet Tanagers, and some flycatchers occur normally in woodland habitats and feed primarily on foliage dwelling insects. More Scarlet Tanagers were observed (296) than all other species combined (274). Furthermore, the tanagers suffered the greatest mortality, accounting for 83.5% of the 85 birds found dead along the roadways.

About 4 times as many birds were observed per hour of travel along Interstates as on secondary highways, probably due to several factors. Birds are more conspicuous along Interstates because of the wide expanses of mowed shoulders, while on secondary roads, dead birds may be thrown into roadside vegetation and live birds can take refuge in the forest edge. Because Interstates have greater surface area of pavement, shoulder, and mowed lawn, they may provide more feeding habitat and thus may attract birds during periods of inclement weather. Finally, both Interstate highways surveyed were located in the major river valleys at elevations of approximately 250 m, while many of the secondary roads traversed higher ground (300–500 m). Our observations from Hubbard Brook Experimental Forest (500 m elev.) indicated that
Table 2

Temporal Variation in Tanager Occurrence and Mortality Along Vermont and New Hampshire Highways, 26 May to 1 June 1974

<table>
<thead>
<tr>
<th>Date</th>
<th>Total Distance (Km) (Duration of Survey in Hours)</th>
<th>Number of Tanagers</th>
<th>Total Tanagers Per Hour of Travel</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Live gender</td>
<td>Dead gender</td>
<td>Live gender</td>
</tr>
<tr>
<td>26 May</td>
<td>60 (0.8)</td>
<td>41</td>
<td>3</td>
</tr>
<tr>
<td>27 May</td>
<td>34 (0.8)</td>
<td>13</td>
<td>7</td>
</tr>
<tr>
<td>28 May</td>
<td>92 (2.0)</td>
<td>10</td>
<td>3</td>
</tr>
<tr>
<td>29 May</td>
<td>302 (5.8)</td>
<td>99</td>
<td>25</td>
</tr>
<tr>
<td>30 May</td>
<td>66 (1.0)</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>1 June</td>
<td>29 (0.4)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Totals</td>
<td>582 (10.8)</td>
<td>164</td>
<td>42</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td>164</td>
<td>42</td>
</tr>
</tbody>
</table>

Few if any tanagers remained in this forest after 26 May (see below), those tanagers that had arrived earlier having either died or moved away, perhaps to the lower valleys and thus to the Interstates.

No tanagers or other forest species were observed along roads between 23 and 25 May. The first and maximal number of tanagers occurred on 26 May when 60.2 tanagers were observed per hour of travel (Table 2). On subsequent days, the numbers generally declined through 1 June. The percentage of live tanagers decreased as the event progressed, due to increasing mortality of weak birds, to the return of the more healthy individuals to forest habitats, or both.

Fewer dead tanagers were found along roads in early mornings than in late afternoon (Table 3). This probably resulted from the accumulation of dead birds during the day, the movement of live birds away from the roads during the warmer parts of the day, and/or to the greater volume of traffic in late afternoon. Since the total number of tanagers observed was lowest in late afternoon (Table 3), it seems likely that the more vigorous birds had left the highways at that time probably to roost in nearby forests for the night.

Stomachs of 14 tanagers found dead along the roadsides contained primarily ants, beetles, and earthworms, all items that probably were obtained by ground feeding. In contrast, the usual spring and early summer diet of tanagers consists mostly of wasps, beetles, and lepidopteran larvae (Martin et al. 1951, Prescott 1965) obtained from forest canopies.

Tanager breeding survey.—Bird population densities have been followed continuously since 1969 in the Hubbard Brook Experimental Forest (Holmes and Sturges 1975), a locality near the center of this grounded-tanager phe-
Table 3

HIGHWAY MORTALITY OF SCARLET TANAGERS FROM 26 MAY–1 JUNE 1974 CATEGORIZED BY DIURNAL TIME PERIODS

<table>
<thead>
<tr>
<th>Time</th>
<th>Total Distance (Km)</th>
<th>Total Tanagers Per Hour of Travel</th>
<th>% Alive</th>
</tr>
</thead>
<tbody>
<tr>
<td>05:00–10:30</td>
<td>117 (2.3)</td>
<td>31.9</td>
<td>93.2</td>
</tr>
<tr>
<td>10:30–15:30</td>
<td>179 (3.2)</td>
<td>45.6</td>
<td>80.6</td>
</tr>
<tr>
<td>15:30–21:00</td>
<td>286 (5.3)</td>
<td>14.7</td>
<td>51.3</td>
</tr>
<tr>
<td>Totals</td>
<td>582 (10.8)</td>
<td>27.5</td>
<td>76.0</td>
</tr>
</tbody>
</table>

nomenon (Fig. 1). In 1974, the first Scarlet Tanagers to arrive at Hubbard Brook were recorded on 15 May. By 23 May, 3 to 4 males, the normal number occupying our main 10 ha census plot, were actively establishing territories and singing, and we frequently saw or heard tanagers in other areas of the forest. Only a few females had arrived by this time. When we next censused, during a break in the rain on 27 May, no tanagers were recorded on the census plot, nor anywhere in the forest. On that day, 2 dead males were found along a dirt road within the forest about 5 km from the Pemigewasset River Valley and Interstate 93. There was no evidence that they had been killed by cars; their stomachs were empty and we surmised that they had died of starvation or exposure. On 29 May, another dead male tanager was found on the forest litter in an undisturbed section of the forest, about 1 km from the end of a dirt road. Its stomach contained only 2 partly expanded but still rolled beech (Fagus grandifolia) leaf buds. There were no signs of bruises or physical damage on the tanager carcass. No other bird species seemed to have disappeared from the forest as completely as had the tanagers, although the numbers of all species on the census records during this time were low. No other species were found dead in the forest.

Between 2 and 6 June, several male and female tanagers reappeared on the census plot and in the forest in general, and nesting was underway shortly thereafter. The breeding density of tanagers that year was about ½ that of the previous 2 years and about ½ of the 1969–1973 average (Table 4). Tanager nesting success in 1974, although hard to assess accurately, appeared to be poor. Perhaps because of low breeding success and the high spring mortality of adults, the densities of breeding tanagers in the 2 subsequent seasons have been about ½ of the 1969–1973 average, the lowest in the 8 years of study at this locality (Table 4).
Table 4

Breeding Populations of Scarlet Tanagers on a 10 ha Plot in Hubbard Brook Experimental Forest, West Thornton, New Hampshire, from 1969 to 1976

<table>
<thead>
<tr>
<th>Year</th>
<th>Individuals Per 10 ha</th>
<th>Breeding Pairs Per 10 ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>1969</td>
<td>4.0</td>
<td>2.00</td>
</tr>
<tr>
<td>1970</td>
<td>6.0</td>
<td>3.00</td>
</tr>
<tr>
<td>1971</td>
<td>5.0</td>
<td>2.50</td>
</tr>
<tr>
<td>1972</td>
<td>8.0</td>
<td>4.00</td>
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<tr>
<td>1973</td>
<td>7.0</td>
<td>3.50</td>
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<tr>
<td>1974</td>
<td>4.0</td>
<td>2.00</td>
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<tr>
<td>1975</td>
<td>2.5</td>
<td>1.25</td>
</tr>
<tr>
<td>1976</td>
<td>1.5</td>
<td>0.75</td>
</tr>
</tbody>
</table>

Discussion

Cause.—The habitat shift and occurrence of tanagers and certain other birds along roadsides in this late May period was correlated with, and lagged slightly behind, a period of cool rainy weather (Fig. 2). Persistent rainfall and/or low temperatures had a depressing effect on the activity of flying insects, as indicated by the numbers of insects captured in Malaise traps that were operating in the Hubbard Brook forest (Fig. 2). We feel that the reduced availability of aerial insects in the forests may have been a prime reason why the tanagers and possibly other species shifted their feeding into areas such as roadsides and lawns where they could obtain food more readily. This may have been particularly effective at this time in late May when these tanagers had just recently completed or were nearing completion of their northward migration.

Other observers have noted that birds often are attracted to the numerous insects that they find washed onto roads by heavy rains (e.g. Finnis 1960). In addition, earthworms and insects driven out of the ground by rain may be more visible to birds along roads and road shoulders (Kent 1974). The occurrence of more tanagers along the Interstates than along secondary highways, given the greater surface area of pavement, shoulder, and mowed lawn associated with Interstates, further supports this hypothesis.

One problem which the food (or any other) explanation for this phenomenon must address is that of the disproportionate effect on Scarlet Tanagers, relative to the other types of forest birds. It may be that this inclement weather occurred at the peak of the tanager migration which seems to be slightly later through this region than the peak migration periods of many other species (Holmes pers. observ.). As a result, tanagers may have been
Fig. 2. Roadside occurrence of Scarlet Tanagers, relative abundance of insects, and mean daily precipitation and temperature in central New Hampshire, 20 May–2 June 1974. Insect data are from Malaise traps operating in undisturbed northern hardwoods, Hubbard Brook Experimental Forest, West Thornton, N.H. (500 m elevation).

less firmly attached to breeding sites and thus could shift more easily to better feeding areas on lawns and along roadsides. However, tanagers that had arrived previously and had been advertising territories in the forest for a week or more either died or left their territories in late May. Why didn’t other species such as warblers and vireos also desert the forest in equally large numbers for better feeding areas?

We suggest that large insectivorous birds may be more severely affected than smaller ones under these circumstances, because of their greater dependence on relatively large-sized insect prey (cf. Hespenheide 1975) which are normally relatively rare in the environment and which may be particu-
larly depressed in abundance during cool wet weather. This would also be related to the greater absolute metabolic needs of large birds, requiring a greater total intake of kcal per bird per day. Since the Scarlet Tanager is one of the larger insectivorous species in these forests feeding actively on flying adult insects (Prescott 1965; Holmes pers. observ.), it may be affected first or more severely than other species. This idea gains support from the fact that the Eastern Kingbird, another large flycatching species, was also strongly affected by this inclement weather. Although no habitat shift was involved, kingbirds were more abundant along the roadsides (see Table 1) and were seen feeding on the ground and road surfaces more often during, than either before or after, this period of inclement weather. Thus, we suggest that reduced availability of large prey items most suitable for large insectivorous birds, coupled with their greater absolute metabolic needs, might force the larger species to shift habitats sooner than the smaller ones. To evaluate these ideas further, more information is needed on the food selection processes of forest birds and on the responses of these species to changing food availabilities and climatic fluctuations.

Long term effects on Scarlet Tanager populations.—Finch (1975b) noted that the cold, wet weather of late May 1974 may have had a measureable effect on the nesting populations of certain species, notably Scarlet Tanagers and Swainson’s Thrushes. Based on the results of the North American Breeding Bird Survey, Robbins and Erskine (1975) report that Scarlet Tanagers population declined 30% in New Hampshire and 50% in Maine in 1974 compared to those in the previous summer. In our 10 ha study area in the Hubbard Brook forest, we recorded fewer breeding pairs of tanagers during June and July 1974 as compared with the 5 previous summers (see Table 4) and nesting success was poor. In the summers of 1975 and 1976, even fewer tanagers were present. These findings suggest that the inclement weather of late May 1974 may have contributed to a significant several-year reduction in local Scarlet Tanager breeding populations at this locality.

SUMMARY

Roadside occurrence and mortality of Scarlet Tanagers and other insectivorous birds are described in relation to unseasonably cold wet weather in late May 1974 in New Hampshire and Vermont. More tanagers were observed in 41 roadside surveys than individuals of all other species combined, and 83.5% of the dead birds found were Scarlet Tanagers. Total numbers of tanagers observed per hour of travel were greater along Interstate than on secondary highways. The percentage of live tanagers on the roadsides decreased by mid-day.

Reduced availability of forest insects because of persistent rains and cool temperatures is considered to be the prime reason for tanagers shifting from forest habitats to roadsides and lawns, areas where they could obtain food such as ants and earthworms,
more readily. Tanagers may have been forced to desert their normal forest habitat sooner than other insectivorous species because of their relatively large body size, heavy reliance on large adult insects, and high absolute metabolic requirements. The local Scarlet Tanager breeding populations in the Hubbard Brook forest declined by 33% in 1974 over the previous year and by 67% in 1975 and 1976 over the 1969-1973 average, suggesting a possible long term effect of this period of heavy mortality.

ACKNOWLEDGMENTS

We thank M. A. Cincotta, F. W. Sturges, C. P. Black, and T. W. Sherry for their enthusiastic help in the surveys. Dr. Robert Chaffee of the Montshire (formerly Dartmouth College) Museum provided information on tanager occurrence in the Connecticut River Valley. J. Elkinton, M. A. Cincotta, and R. Bonney made many helpful comments on early drafts of the paper. The work in the Hubbard Brook Experimental Forest is supported by grants from the National Science Foundation to Dartmouth College.

LITERATURE CITED


EDITORIAL: CHANGING OF THE GUARD

With this issue, my tenure as editor of The Wilson Bulletin is completed. I have enjoyed and learned much from having edited our journal and I hope that in some small way I have contributed to the success of the Society. Editing is a very time-consuming and often frustrating task, but it was made more enjoyable for me by the large measure of cooperation that I had from authors, referees, officers of the Wilson Society, editorial assistants, secretaries, and very importantly, Allen Press. During the past four years several hundred ornithologists contributed time and expertise to review manuscripts submitted to the Wilson Bulletin. Their efforts have made the Wilson Bulletin what it is today. I owe particular thanks to Lyda Eubank who, as one of our departmental secretaries, has handled much of the filing and correspondence associated with editing the Wilson Bulletin. Mississippi State University generously supported my editorial duties by providing office space and secretarial time for the Society. Ken Blair, our liaison at Allen Press, has contributed immeasurably over the years to the technical aspects of getting the journal out. I'm also aware of and grateful to the many “unknown” employees of Allen Press for a job well done.

To all who submitted manuscripts to the Wilson Bulletin—thanks for your perseverance and cooperation with the editorial process. To those whose manuscripts were rejected, I offer encouragement. Have faith in the peer review process. Make rejection a learning experience and do not let it dampen your enthusiasm in seeking new knowledge about birds. Perhaps a referee was wrong. I know I made mistakes—both in accepting and rejecting some manuscripts. While there are bound to be editorial errors made, I also feel that I’ve learned from my failures. We can all take some consolation in the strength of our profession and in the multitude of publication alternatives available to us. It has been particularly interesting to me to see which of the manuscripts rejected from the Wilson Bulletin eventually appeared in one of our sister journals and which rejected by one of them was eventually published in the Wilson Bulletin. To our new editor, Jon Barlow, I wish every success. He is full of enthusiasm and brings great expertise to the job. Support him.

JEROME A. JACKSON
COMMUNITY ECOLoGY OF THE HELMINTH PARASITES OF THE BROWN PELICAN

Stephen R. Humphrey, Charles H. Courtney, and Donald J. Forrester

Research on the dynamics of communities can be very rewarding, for it can reveal the processes that determine the character of the community. However, some kinds of communities are difficult to observe, so their nature and dynamics remain obscure. Communities of parasites living inside other organisms can be studied only by killing the hosts, enabling only a single, momentary view of the community within each. To learn the dynamics of such a community, it is necessary to build a composite view from a series of samples. Ecologists have found numerical diversity analysis to be a powerful tool for understanding obscure communities through indirect data, for diversity focuses attention on particular species, locations, times of year, or biological processes that are influential in community dynamics. An exemplary study (Hair and Holmes 1975) of parasites in the Lesser Scaup (Aythya affinis) shows the power of diversity analysis by demonstrating spatial displacement of parasites of the small intestine—apparent solutions to competition for shared resources.

The community studied here is the helminth fauna (Courtney and Forrester 1974) of the Brown Pelican (Pelecanus occidentalis). Careful inspection of the organs uncovers a separate example of the community for each bird sampled. By choosing replicate samples in different geographic locations and of different host age, it is possible to examine community structure as a function of region and successional age. This paper describes community succession in pelican helminths, provides evidence of competition among the parasites, and suggests host responses that suppress the parasite community, and shows effects of food intake and zoogeography on the community.

METHODS

Fifty-three fledged birds were collected from widely scattered localities on the coasts of peninsular Florida. Nine nestlings were obtained from various colonies on the Atlantic coast, and 30 nestlings were taken from Bird Key (Lee County) on the Gulf coast. Fourteen pelicans that had been shot or found dead on Grand Terre, Louisiana, also were examined. The Louisiana pelicans had been transplanted from the Atlantic coast of Florida as nestlings in 1968, 1969, and 1970. Collections were from 1971 through 1973 and provided no control over possible seasonal cycling of parasite populations. For analysis, the birds were separated into age classes and were grouped into three localities—the Atlantic coast of Florida, the Gulf coast of Florida, and Louisiana. Some birds were examined shortly after death, but most were frozen when received. At necropsy the birds were dissected and the following examined: esophagus, proven-
tricula, duodenum, ileojejunum, ceca, small and large intestine, cloaca, heart, trachea, lungs, liver, gall bladder, kidneys, nasal cavity, orbit, subcutaneous tissues, and body cavity. Procedures for recovering, killing, fixing, and studying helminths were those described by Kinsella and Forrester (1972). Where trematodes were small and numerous, their numbers were determined by mixing them thoroughly with 250 ml of water and counting a 10 ml aliquot.

Two taxonomic problems introduced bias into the subsequent data analysis. We treated all individuals of Contracaeum as 1 species complex, but 2 species were present (C. spiculargerum and C. multipapillatum). The differentiated species occurred about equally in our samples. Phagicola longus and P. sp. cf. minutus were treated as one species. The unidentified species of Phagicola was always accompanied by greater numbers of P. longus and was found only 3 times—twice in Florida Atlantic coast nestlings and once in Florida Gulf coast nestlings.

Comparisons were of helminth communities from fledged birds on all 3 coasts and of helminths from birds in an age series (2 week nestlings to adults) on Florida's Gulf and Atlantic coasts. Communities were evaluated by quantifying the parasite load of each bird age class and measuring the diversity of the communities with indices derived from information theory. Indices used here are for species diversity, $H' = -\sum p_i \log p_i$ (Shannon and Weaver 1949), where $p_i$ is the number of the $i^{th}$ species divided by sample size, and equitability, $E = H'/H_{\text{max}}$ (Sheldon 1969), where $H_{\text{max}}$ is the natural log of the number of observed species. A component of $H'$, $H'_n$, is the contribution to the diversity value by the most abundant species. That is, $H'_n = -p_i \log p_i$. This value (1) makes it possible to judge the importance of each species in its community and (2) in cases where 1 species is overwhelmingly common, establishes a criterion ($H'_{n_i} < H'_{n_2}$) for attributing an inequitable distribution of relative abundances to a superabundant species. In such cases, the apparent disadvantage of the distorted index value is offset by the signal that some environmental resource is inequitably distributed among species. That indicates that the resource occurs in only a few forms or that the most abundant species is exceptionally well adapted to use the resource, or both.

Sample parameters are given in Table 1. The testing of sample size by calculating diversity with successively pooled sample data, as prescribed by Wilhm (1970a), works in a peculiar fashion with parasite communities. Rather than steadily progressing toward an asymptote, parasite diversity values exhibit great variance. This happens because the few extremely heavy infestations that overwhelmingly reduce diversity are likely to occur after many less severe cases are chosen in the random sampling. This seemingly erratic pattern is shown well by our samples. An additional source of variation in our data was the pooling of all birds along one coast as a single sample; no doubt site differences in parasite loads confound our data. Samples as small as 6 birds characteristically approached the asymptotic diversity value, but in such small samples a bird with an atypical infestation could markedly increase or decrease the value. Thus, we are not entirely satisfied with the smaller pelican samples but think that they characterize the parasite communities reasonably well. Our smallest samples, as few as 2 birds, we judged to be inadequate. However, we include them in the results anyway, with trepidation. The endangered status of this bird made larger samples unjustifiable at the time of collection.

THE ORGANISMS

Like the declining Pacific coast subspecies, some eastern populations of the Brown Pelican also have declined recently. In Texas, only 18 young were produced in 1963
(Webster 1963). Indigenous wild pelicans have not nested in Louisiana since 1961, though pelicans brought to Louisiana from Florida as flightless nestlings in 1968, 1969, 1970, and 1971 nested when they were 3 years old (Williams and Joanne 1974). Only 1 small colony exists in North Carolina (Wray and Davis 1959). In South Carolina the population apparently has declined, but this may be due to the gradual eroding of the nesting site at Deveaux Banks (T. A. Beckett, pers. comm. cited by Schreiber and Risebrough 1972). Pelicans have not been known to nest in Georgia (Burleigh 1958), Alabama (Imhof 1976), or Mississippi (Burleigh 1944) in recent years.

In the United States, only Florida has a stable population of Brown Pelicans. During 1968–74 biologists of the Florida Game and Fresh Water Fish Commission made visits and aerial surveys of all colonies in the state. Nesting occurred in 30 colonies; all but one colony (at Port St. Joe) were on islands off the Florida peninsula. There appeared to be a relatively stable population of between 11,000 and 16,000 adult pelicans (Williams and Martin 1968, 1970; Nesbitt et al. 1977).

Thirty-one species of helminths were found in the pelicans (Courtney and Forrester 1974). Most were rare, contributing importantly to the diversity of the helminth community but having minor impact on the health of the host. Only 6 species were frequent enough to be considered as consistently dominant community members. One of these inhabited the proventriculus, 4 the small intestine, and 1 the kidneys. Most of these helminths enter the pelicans as intermediate forms within ingested food. These then mature into adult forms of the parasites. An exception to this pattern is *Contracaecum*, which enters both as an intermediate form as above and as an adult, by direct transfer from parent pelicans by regurgitative feeding of nestlings.

*Contracaecum multipapillatum* and *C. spiculigerum* (Nematoda: Heterocheilidae; treated as 1 taxon hereafter) live in the proventriculus, where they may be free or attached to the mucosa. The life cycles of several species of *Contracaecum* were determined by Huizinga (1965). Eggs hatch into ensheathed second-stage larvae in 5 to 7 days. Larvae of both species infect transport hosts, the copepods *Triigriopus californicus* and *Cyclops vernalis*. *C. multipapillatum* requires a transport host, but the cosmopolitan *C. spiculigerum* can directly infect the intermediate hosts, fish. Larvae hatch and molt to the third stage in the intermediate hosts, a guppy (*Lebistes reticulatus*) and a killifish (*Fundulus heteroclitus*). After ingestion by the pelican, *Contracaecum* undergo no tissue migration and survive about 90 days (Huizinga 1971).

The 4 most common parasites of the small intestine were the trematodes *Mesostephanus appendiculatoides* (Cyathocotylidae); *Phagicola longus*, *P. sp. cf. minutus*, and *Galactostomum darbyi* (Heterophyidae); and *Stephanopora denticulata* (Echinostomatidae).

The Brown Pelican is the only known final host of *M. appendiculatoides*. The first intermediate host is the marine snail, *Cerithium muscarum*, and the second intermediate hosts are mullet, *Mugil* spp. Pelicans become infected by eating mullet (Hutton and Sogandaeres-Bernal 1960a).

The most abundant and ubiquitous helminth found in this study was the trematode, *Phagicola longus*. The first intermediate host is unknown but may be a hydrobiid snail (R. W. Heard, pers. comm.). The second intermediate hosts are mullet, in which metacercaria inhabit the heart muscle in great numbers and less commonly the intestinal wall and muscle (Hutton and Sogandaeres-Bernal 1959). *Phagicola* undergo a brief tissue migration in the intestine of the Brown Pelican (Ciurea 1924).

The life cycle of *G. darbyi* is unknown. Mature *S. denticulata* occur in several species of water birds in Florida (Courtney 1973). The metacercaria have been found (Stunkard and Uzmann 1962) in a killifish, *Fundulus heteroclitus*. 
## Table 1
### Sampling Parameters, Diversity, and Equitability of Helminth Communities from Florida and Louisiana

<table>
<thead>
<tr>
<th></th>
<th>No. of Pelicans</th>
<th>No. of Parasite Species</th>
<th>No. of Parasite Individuals</th>
<th>No. of Parasites/Bird</th>
<th>H'</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Total Pelicans</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Florida, Louisiana</td>
<td>106</td>
<td>28</td>
<td>756,238</td>
<td>7,134</td>
<td>0.640</td>
<td>0.192</td>
</tr>
<tr>
<td><strong>Fledged</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Florida Atlantic coast</td>
<td>39</td>
<td>20</td>
<td>391,159</td>
<td>10,030</td>
<td>0.458</td>
<td>0.143</td>
</tr>
<tr>
<td>Florida Gulf coast</td>
<td>14</td>
<td>15</td>
<td>73,472</td>
<td>5,248</td>
<td>0.864</td>
<td>0.319</td>
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<tr>
<td>Louisiana coast</td>
<td>14</td>
<td>12</td>
<td>167,843</td>
<td>11,989</td>
<td>0.074</td>
<td>0.030</td>
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<tr>
<td><strong>Florida Atlantic coast</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nestlings 4.5 weeks</td>
<td>2</td>
<td>7</td>
<td>2,171</td>
<td>1,086</td>
<td>0.876</td>
<td>0.450</td>
</tr>
<tr>
<td>Nestlings 7 weeks</td>
<td>3</td>
<td>5</td>
<td>7,778</td>
<td>2,593</td>
<td>0.765</td>
<td>0.438</td>
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<tr>
<td>Nestlings 9 weeks</td>
<td>4</td>
<td>9</td>
<td>27,922</td>
<td>6,980</td>
<td>0.704</td>
<td>0.361</td>
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<tr>
<td>Fledged young (12–52 weeks)</td>
<td>5</td>
<td>14</td>
<td>50,183</td>
<td>10,037</td>
<td>0.321</td>
<td>0.122</td>
</tr>
<tr>
<td>Subadults (1–3 years)</td>
<td>27</td>
<td>18</td>
<td>271,895</td>
<td>10,070</td>
<td>0.436</td>
<td>0.151</td>
</tr>
<tr>
<td>Adults (&gt;3 years)</td>
<td>7</td>
<td>17</td>
<td>69,083</td>
<td>9,869</td>
<td>0.390</td>
<td>0.138</td>
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<tr>
<td><strong>Florida Gulf coast</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nestlings 2 weeks</td>
<td>6</td>
<td>4</td>
<td>1,094</td>
<td>182</td>
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<tr>
<td>Nestlings 3 weeks</td>
<td>6</td>
<td>4</td>
<td>3,180</td>
<td>530</td>
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<tr>
<td>Nestlings 4.5 weeks</td>
<td>6</td>
<td>9</td>
<td>14,002</td>
<td>2,334</td>
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<td>Nestlings 7 weeks</td>
<td>6</td>
<td>8</td>
<td>28,836</td>
<td>4,806</td>
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<td>Nestlings 9 weeks</td>
<td>6</td>
<td>10</td>
<td>26,044</td>
<td>4,341</td>
<td>0.961</td>
<td>0.417</td>
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<td>Fledged young (12–52 weeks)</td>
<td>3</td>
<td>11</td>
<td>25,471</td>
<td>8,490</td>
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<td>0.093</td>
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<td>Subadults (1–3 years)</td>
<td>4</td>
<td>12</td>
<td>21,801</td>
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<td>Adults (&gt;3 years)</td>
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<td>26,199</td>
<td>3,743</td>
<td>0.959</td>
<td>0.374</td>
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<td><strong>Louisiana coast</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fledged young (12–52 weeks)</td>
<td>3</td>
<td>7</td>
<td>56,915</td>
<td>18,972</td>
<td>0.120</td>
<td>0.062</td>
</tr>
<tr>
<td>Subadults (1–3 years)</td>
<td>5</td>
<td>7</td>
<td>66,988</td>
<td>13,398</td>
<td>0.034</td>
<td>0.017</td>
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<tr>
<td>Adults (&gt;3 years)</td>
<td>6</td>
<td>10</td>
<td>43,935</td>
<td>7,322</td>
<td>0.062</td>
<td>0.027</td>
</tr>
</tbody>
</table>

The kidney fluke, *Renicola thapari*, is found in both Brown and White pelicans (*Pelecanus erythrorhynchos*; Courtney 1973). Its life cycle is unknown.

**RESULTS**

The diversity of Brown Pelican helminth communities (Table 1) was very low in all cases. Values for fledged birds ranged from 0.074 to 0.364. High-
Table 2
CONTRIBUTION TO COMMUNITY DIVERSITY (H'\(n\)) OF ECOLOGICALLY DOMINANT HELMINTHS

<table>
<thead>
<tr>
<th>Location</th>
<th>2 Weeks</th>
<th>3 Weeks</th>
<th>4.5 Weeks</th>
<th>7 Weeks</th>
<th>9 Weeks</th>
<th>Fledged Young</th>
<th>Subadults</th>
<th>Adults</th>
</tr>
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<tr>
<td>Florida Gulf coast</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M. appendiculatoides</td>
<td>.012*</td>
<td>.020*</td>
<td>.228*</td>
<td>.123*</td>
<td>.348</td>
<td>.082</td>
<td>.367</td>
<td>.368</td>
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<tr>
<td>P. longus</td>
<td>–</td>
<td>–</td>
<td>.345</td>
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¹ TR = presence in trace amounts.
* H'\(n1\) < H'\(n2\).

est diversity was 1.095 in subadults from the Florida Gulf coast, and the least diverse sample was 0.034, subadults from the Louisiana coast. Such low diversities are comparable to those found in the benthic macroinvertebrates of polluted streams (Wilhm 1970b). Equitability values also were very low—0.45 for the most equitable sample.

The reason for this low diversity and inequitable distribution of relative abundances is that every sample was dominated by a superabundant species (H'\(n1\) < H'\(n2\), Table 2), either M. appendiculatoides or P. longus. The former species invades nestlings and is superabundant during the early weeks, but at 7 to 9 weeks of age P. longus populations become dominant and superabundant. Other flukes of the small intestine, G. darbyi and S. denticulata, were consistent though minor members of the helminth communities. These were most important in fledged birds. S. denticulata was most im-
Fig. 1. Diversity of helminth communities in seral ages of the Brown Pelican.

Important in Louisiana pelicans, from which *M. appendiculatoides* was absent. Change of diversity during community succession (Fig. 1) deviated from the expected pattern of increase with seral age. Diversity increased from young to older nestlings, decreased markedly in fledged young, increased again in the subadult years, and then dropped slightly in sexually mature birds. However, no increase in diversity occurred in subadult and adult birds from the Louisiana coast. Probably these changes correspond with major events in the life history of the host. Helminth communities in subadult and adult pelicans differed distinctly among the 3 regions, with highest diversity at the Florida Gulf coast and lowest at the Louisiana coast. A striking measure of the low diversity in Louisiana birds was the absence of 10 parasite species that occurred in Florida birds (Courtney and Forrester 1974).

The main features of parasite community succession are shown in Fig. 2. Most parasite species were very rare, and only *M. appendiculatoides*, *P. longus*, and *Contracaecum* occurred in numbers large enough to illustrate ecological processes.

*M. appendiculatoides* in the Florida Gulf coast comprised almost all of the parasite infection of 2-week-old pelicans, with abundance not exceeding
Fig. 2. Frequency and number of the most abundant helminths in Brown Pelicans from three regions. Bars show the major features of parasite community succession as a function of host age.

about 500 per bird. The importance of this fluke remained high and loads increased to 4000 per bird at 7 weeks. Frequency and numbers decreased to insignificant levels in fledglings and then increased to moderate proportions in subadults and adults, with about 1000 per bird. Among Florida Atlantic coast birds, *M. appendiculatoides* infections remained at about 1000 per bird from nestlings to adults, with relative abundance diminishing from moderate to low levels as other parasites became more common. In Louisiana, *M. appendiculatoides* was absent from fledged young and subadults and occurred in very small numbers among adults.

*P. longus* was absent from young nestlings but occurred as up to half the total parasites and 1000 per bird when nestlings were 4–5 weeks old. This fluke quickly reached enormous numbers, up to 3000 per bird on the Florida Gulf coast, 10,000 on the Florida Atlantic coast, and over 18,000 on the Louisiana coast. In all cases, the largest populations occurred among fledged young, with a decrease in subadult and adult classes. Infections were slightly lower (9000 per adult) on the Atlantic coast but were reduced substantially (2000 per adult) along the Florida Gulf coast.

*Contracaecum* was a minor community member in birds of both young
DISCUSSION

Low diversities and the superabundance of *M. appendiculatoides* and *P. longus* show that few parasites are well adapted to exploit the pelican resource. Of the 2 that are highly successful, *M. appendiculatoides* is specific to Brown Pelicans as a final host, whereas *P. longus* occurs also (Hutton and Sogandares-Bernal 1960b) in the Great Egret, *Casmerodius albus*. Host generalists such as *S. denticulata* do not achieve large populations in the Brown Pelican.

Zoogeography.—Effects of zoogeographic processes are evident from an unintentional faunistic “experiment.” Between 1958 and 1961 the last nesting Brown Pelicans in Louisiana were extirpated. In 1968 and subsequent years, 12-week-old nestlings were introduced from colonies on the Atlantic coast of Florida. These birds were fed at the release site to enhance survival, and they were not chemically treated to eliminate parasites. The new pelican population began to reproduce in 1971.

The low helminth diversity found in Louisiana may have resulted from this history of extirpation and reintroduction. Several of the parasites expected in pelicans probably became rare or extirpated during the years when pelicans were absent from this region. Introduced birds probably brought *M. appendiculatoides* with them, and adults now include a few in their internal faunas. However, the life cycle appears to have been broken by the loss of intermediate forms of *M. appendiculatoides* in Louisiana mullet, and the few adult flukes introduced in infected birds may be insufficient to re-establish a complete life cycle. The kidney fluke *R. thapari* is now absent from Louisiana, though present in some numbers in the Florida portion of the Gulf coast. Other helminths present on either coast of Florida but absent off Louisiana include *Cyathostoma phenisci*, *Capillaria* sp. cf. *mergi*, *Galactostomum fregatae*, *G. darbyi*, *Echinochasmus* sp. cf. *dietzevi*, *Austrobilharzia terrigalensis*, *Carneophallus turgidus*, *Parvitaenia ibisae*, and an unidentified schistorophid larva.

By contrast, Louisiana pelicans had vast numbers of *P. longus*. This fluke no doubt persisted in Louisiana during the pelicans’ absence, inasmuch as an alternate final host (the Great Egret) was present continuously.

The other striking regional difference in diversity is in adult pelicans, which have relatively diverse parasite communities on the Florida Gulf coast but comparatively poor communities on the Atlantic coast (Table 1). Though
this pattern probably reflects a fundamental difference in pelican habitat in the 2 areas, we cannot determine its nature. Because the parasites are acquired from fish, it seems reasonable to suppose that the 2 coasts differ substantially in the relative abundance of fish taxa used as food or that environmental factors cause contrasting phenologies of fish reproduction and movement.

Food web interactions.—Though actual changes in diet as pelicans become older are unstudied, changes in parasite communities derived from food organisms indicate several dietary patterns. The observed increase in helminth diversity with advancing age of pelican nestlings would be expected if birds progressively feed on larger fish of greater taxonomic diversity. Sharp decline of diversity in fledglings occurs when young birds are learning to feed themselves, so food intake may be low or concentrated on a few prey species. This diversity change results from explosive growth of P. longus populations, indicating heavy dependence on mullet (the second intermediate host) as food during this period.

The decline of Contracaecum in fledgling pelicans probably reflects prey selection by the fledglings in place of selection by parent birds. Because these parasites survive only about 90 days (Huizinga 1971), their numbers depend on continual ingestion of infected hosts. An age immunity effect may also reduce the parasite numbers.

Competition.—The unusually depauperate helminth community in Louisiana pelicans reveals patterns (Fig. 2) from which we infer the importance of interspecific competition among parasites. The Louisiana samples contain almost no M. appendiculatoides but enormous numbers of P. longus. In contrast, Florida birds are infected with moderate M. appendiculatoides populations and substantially smaller P. longus populations. We interpret the success of P. longus in Louisiana birds as attributable to lack of interspecific competition from M. appendiculatoides. Both trematodes occupy the same portion of the small intestine, and M. appendiculatoides is about 3 times as large as P. longus, so the former should have an energetic impact that is disproportionate to its numbers.

Another intestinal trematode, S. denticulata, also is more abundant (48 flukes per adult bird) in Louisiana than in Florida. This fluke is about 10 times the size of P. longus. Again, we judge the success of S. denticulata in Louisiana pelicans to result from low competition in the absence of M. appendiculatoides. Our interpretation is further supported by the observations that S. denticulata is rare (2 flukes per adult) in Florida Gulf coast pelicans, in which M. appendiculatoides is most numerous, but is more common (19
flukes per adult) in Florida Atlantic coast pelicans having fewer *M. appendiculatoides*.

Similarly, the reduction of *M. appendiculatoides* in pelicans of both Florida coasts probably results from competition with *P. longus*. These 2 undergo a shift in dominance that is evident in the 7 and 9 week stages in Fig. 2 and Table 2.

Presumably competition among flukes in the more diverse Florida communities operates by reducing the survival rates of parasites after they have been ingested. Importantly, such competition also indicates the likelihood of competition between parasites and the host birds for some nutrients.

Development of immunity by the host.—Eventual decline of *P. longus* populations in adult pelicans (Fig. 2) may reflect development of age immunity, for no other small intestinal parasites remain abundant, so the decline cannot be attributed to competition. Differences in the amount of decline of this parasite among pelican populations may be explained by differences in parasite loads established in fledglings and differing levels of competition from *M. appendiculatoides*, especially during the subadult years. *P. longus* metacercaria from mullet must encyst in pelican intestinal mucosa in order to mature. During this brief tissue-dwelling stage they make a good target for an immunological response by the host. Parasites like *M. appendiculatoides*, which apparently remain in the lumen without entering intestinal tissue, offer less opportunity for immunological counter-measures.

An alternative explanation (which we cannot evaluate) of the *P. longus* decline is that pelicans surviving longest and thus best represented in the adult age class are those that avoid mullet in their diets.

Management.—Heavy infection of Louisiana pelicans by *P. longus* might be a serious problem worth avoiding in future reintroduction efforts. A factor probably contributing to the imbalance between *P. longus* and *M. appendiculatoides* was that introduced birds came from the Atlantic coast of Florida, where considerable imbalance prevailed (Fig. 2). Pelicans from the Gulf coast of Florida, in which both of these trematodes have reached moderate numbers and evidently balanced populations, may be more fit candidates for reintroduction.

**SUMMARY**

Helminths from *Pelecanus occidentalis* were described as communities of several successional ages and of 3 geographic regions. Community diversity was uniformly low, resulting from enormous numbers of *Mesostephanus appendiculatoides* in young hosts and *Phagicola longus* in old birds. Regional differences in diversity are attributed to unknown features of pelican habitat along Florida coasts and a history of pelican
extirpation and reintroduction on the Louisiana coast, which appears to have caused extirpation of some parasite taxa. Seral changes in parasites indicate increasing diversity of food items as nestlings grow, sudden heavy feeding on mullet (Mugil spp.) at fledging, and apparent avoidance of other fish species by fledged birds. The success of P. longus populations in Louisiana birds is attributed to a lack of interspecific competition from M. appendiculatooides. Eventual decline of P. longus populations in adult pelicans may reflect development of age immunity, though other explanations are possible. Success of efforts to reintroduce pelicans into formerly occupied range may be enhanced by selecting birds with balanced parasite communities.

ACKNOWLEDGMENTS

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FLORIDA STATE MUSEUM, UNIV. OF FLORIDA, GAINESVILLE 32611. COLLEGE OF VETERINARY MEDICINE, AUBURN UNIV., AUBURN, AL 36830. LABORATORY OF WILDLIFE DISEASE RESEARCH, COLLEGE OF VETERINARY MEDICINE, UNIV. OF FLORIDA, GAINESVILLE 32610.
NEST-SITE SELECTION OF WILLETS IN A NEW JERSEY SALT MARSH

JOANNA BURGER AND JOSEPH SHISLER

Willets (Catoptrophorus semipalmatus) breed along the east and west coasts of North America (American Ornithologists' Union 1957); nesting in a variety of habitats including beaches, edge areas, and salt marshes. Willets gather on communal display areas over bare ground or marshes, and then scatter into the surrounding areas to nest (Palmer 1967). They defend nesting territories, and either feed within them or defend nearby feeding territories (Vogt 1933, Tomkins 1965). Tomkins (1965) mentioned the opposing tendencies for gregariousness and territorial spacing, which together should result in uneven distribution of nesting pairs in discrete flock groupings within the available habitat. However, the nesting pattern of Willets has not been documented despite their commonness along our coasts.

We studied nest-site selection of Willets in a salt marsh in southern New Jersey with particular emphasis on the environmental and social determinants of nest-site selection. Many of the marshes in this area contain mosquito ditches. We selected an area large enough to include ditched and unditched marsh to allow determination of the effect of ditching on nesting.

METHODS AND STUDY AREA

We examined a 20 ha salt marsh near Tuckerton, New Jersey (33°30'N, 74°21'W). Spartina patens and S. alterniflora dominated the marsh, although a few Iva frutescens and Baccharis halimifolia bushes grew on some higher areas (spoil piles). We distinguished the short form of S. alterniflora (< 50 cm) from the tall form (> 50 cm) since it is physiognomically distinct. The marsh contained approximately 1720 m of ditches constructed in 1970 by the Ocean County Mosquito Commission. They graded the spoil from the 0.65 m wide ditches over the marsh surface leaving the spoil only a few cm higher than the surrounding marsh. Spoil piles always occurred adjacent and parallel to the ditches. Spoil piles, the highest areas in the marsh, were never inundated by tidal water during this field season. During 2 storm tides water covered most of the rest of the marsh, although the higher S. patens areas remained dry under normal tidal conditions.

We mapped the vegetation in the study area from aerial photographs, aerial surveys by helicopter, and ground surveys, and monitored the area periodically to determine the peak of nesting activity. Four field observers surveyed the area and located 18 nests on 28 May 1976. We mapped the location of each nest (Fig. 1), and recorded the following data: clutch size, egg size, dead grass cover, mean height of live and dead grass, and distance to the nearest bush, ecotone, water, spoil pile, and Willet nest. We collected similar data from 20 points located in the study area selected from a table of random numbers.
RESULTS

Environmental determinants of nest-site selection.—In the study area, most Willets nested in the northern section containing the most ditches. Few Willet nests occurred in an equivalent sized area completely devoid of ditches but otherwise similar in vegetation.

Half of the nests occurred in *S. patens* and half occurred in *S. alterniflora*.
\( \chi^2 = 4.5 \), d.f. = 2, N.S.). Since ditches dominated much of the marsh where they nested, we wondered if Willets required ditches near nest sites. Therefore, we compared the percentage of ditching with the number of nests in each vegetation area but found no significant association \( \chi^2 = 2.26 \), d.f. = 2, N.S.).

Twelve of the 18 Willets built nests on spoil piles, 5 nested within 20 m and 1 pair nested 50 m from a spoil pile. The nests were significantly closer to spoil piles than were the random points \( \chi^2 = 153.5 \), d.f. = 4, \( p < 0.001 \). Secondly, the number of Willet nests actually on spoil piles differed significantly from the random points \( \chi^2 = 283 \), d.f. = 1, \( p < 0.001 \). Thus, Willets tended to nest on or near spoil piles.

Since spoil piles always occur next to ditches, Willets may be selecting nest sites close to water rather than on the spoil piles. If water were the salient feature, then some Willets should nest near natural water areas. Several small pools dotted the area but Willets did not nest next to these. Secondly, if they preferred water and not the spoil piles, then some birds should have nested just off the piles near the water. This, however, did not occur.

All bushes on the study area grew on the spoil piles, suggesting that Willets may be selecting nest sites close to bushes. Willets on spoil piles, however, did not nest close to bushes \( (\bar{x} \text{ distance} = 6.1, \text{ S.E.} = \pm 1.6 \text{ m}) \). The mean distance to bushes of all Willet nests \( (8.1 \pm 2.74 \text{ m}) \) did not differ significantly from that of the random points \( (\bar{x} = 6.8 \pm 0.68 \text{ m}, t = 1.21, \text{ d.f.} = 35, \text{ N.S.}) \).

We then compared vegetational characteristics of the Willet nests with those of the random points. The means for Willet nests did not differ significantly (t values less than 1.3) from the random points with respect to percentage of live vegetation (53% vs 54%), percentage of dead vegetation (46% vs 43%), height of live vegetation (31 vs 30 cm) and height of dead vegetation (22 vs 14 cm). Thus, Willets nest randomly with respect to vegetational characteristics, species of vegetation, distance to bushes, and distance to water. They preferred to nest on the spoil piles regardless of the surrounding vegetation.

Social behavior determinants of nest-site selection.—We compared the nearest neighbor distances of the Willet nests with those of the random points within the entire nesting area. The mean internest distance of Willets was much lower \( (41.2 \pm 32 \text{ m}) \) than that of the random points \( (58.7 \pm 46 \text{ m}) \) and they nested closer together than expected by chance \( (\chi^2 = 17.2, \text{ d.f.} = 5, p < 0.005) \). Only 2 Willets \( (11\%) \) nested farther than 50 m from a neighbor, compared to 6 \( (33\%) \) of the random points. Thus, considering the entire nesting area, Willets clumped while nesting. Their clumping doesn’t appear
to be a function of the clumped ditches since Willets did not nest on the outlying ditches (Fig. 1). Similarly, even within the area of extensive ditching, birds could have nested farther from one another than they did.

We next examined nest spacing in the north end of the study area. Eleven Willets nested along the ditches and 3 nested elsewhere. Using a table of random numbers, we located 3 points in the area. Then we computed the total linear ditching distance (1522 m), and randomly plotted 11 points (equal to the number of nests) along the ditches. We then computed nearest neighbor distances for the random points and compared them to the Willet nests (Fig. 2). The Willets nested farther from each other than expected by chance ($\chi^2 = 21.9$, d.f. = 5, p < 0.001). With the exception of 1 group of 4 nests in S. patens, all Willets nested between 37 and 53 m apart. One of the Willets in this group did not nest on a spoil pile, thus its nest was slightly lower and may not have been as visible as the other 3 nests nearby. The side of the ditch used for nesting made no difference in the distance between neighbors. That is, nearest neighbor Willets nesting on opposite sides of a ditch did not nest significantly closer ($t = 0.56$, d.f. = 11, N.S.) than those on the same side of the ditch ($28 \pm 1.9$ vs $33.6 \pm 12$ m). Since Willets rely heavily on aerial and wing displays (Tomkins 1965, Howe 1974), we did not expect ditches to act as visual barriers for nesting.

Thus, in summary, Willets nested in clumps, spacing themselves with
Fig. 3. Comparison of spoil nests (open rectangle) with natural nests (hatched rectangle) for nesting parameters. Means = horizontal line, standard error = vertical rectangle, and standard deviation = vertical bar.

respect to one another in the preferred nesting area. They preferred to nest on spoil piles and nested randomly with respect to vegetational species, vegetational characteristics, and water.

_Spoil versus natural nests._—We compared the characteristics of Willet nests in natural areas with those on spoil piles (Fig. 3). Features characteristic of ditch construction (i.e. water and bushes) showed significant differences between spoil and natural nests ($F = 32$, d.f. = 1). No differences existed with respect to the distance to the ecotone (here meaning an area of change
in vegetation species). No significant differences existed between spoil and natural nests with respect to vegetational characteristics (F < 1.23).

Willets in this study constructed nests of only S. patens grass, concealing the nest by pulling some of the dead grass over the top to form a dome. We measured the depth of all nests. Willets nesting in natural situations built significantly deeper nests than those nesting on spoil piles (F = 34.5, d.f. = 1, 18, p < 0.005). We then computed egg size using the method of Grossfeld (1937) which takes into account the length and breadth. Willets nesting on spoil piles laid significantly larger eggs than those nesting in natural situations (F = 5.93, d.f. = 1, 46, p < 0.05).

**DISCUSSION**

*Nest-site selection.—* Despite the extensive recent work on shorebirds, little information exists either on general habitat preferences, or on specific nest-site preferences. Graul (1975) analyzed general habitat preferences as well as specific nest-site characteristics for the Mountain Plover, Charadrius montanus. He recorded differences with respect to vegetation species, slope of the ground, and proximity to manure piles. He noted that the spatial relationships of the plover nests suggested that nests were not placed randomly with respect to one another, but he did not test this hypothesis.

In this study we examined general habitat and specific nest-site preferences of Willets nesting in a salt marsh containing mosquito ditches. Willets selected nest sites on spoil piles and nested randomly with respect to vegetation characteristics and distance to bushes and water. Slight elevation differences in the marsh result in different species of vegetation. Tidal waters regularly inundate the low S. alterniflora areas. Presumably, Willet nests and eggs cannot withstand tidal inundations; hence the preference for spoil piles.

Although their absence from these low S. alterniflora areas was not significant, it would have been if we added the extensive marsh area that did not contain any Willets and which was adjacent to our study area.

Considering the entire nesting area, Willets nested closer to one another than expected by chance; but considering only the north end of the study area, the Willets nested farther apart than expected by chance. Thus they spaced out in a clump. This nesting pattern was not an artifact of the ditching pattern because sufficient ditching existed for the Willets to nest either farther or closer than they did. Our data, therefore, support the suggestion of Tomkins (1965) that Willets clump, spacing out within these clumps. Several authors described the social behavior responsible for this nesting pattern (e.g. Vogt 1938, Tomkins 1965, Howe 1974). More marsh area should be examined to confirm the clumping nature of their distribution.
Presumably the clumping provides increased social stimulation for breeding, whereas the spacing relates to predation pressures. Nest density is generally assumed to be a compromise between nesting together for social stimulation and predator mobbing (Kruuk 1964) and nesting far apart for camouflage of the eggs and young (e.g. Tinbergen 1956, Cullen 1960). Evidence for the camouflaged pattern included roofed-over nests, cryptic eggs, cryptic young, and cryptic adults while incubating. Whereas Willets are not noted for mobbing predators, several times we have had 3 or 4 birds fly over our heads at one time.

_Spoil versus non-spoil nests._—Considerable discussion surrounds salt marsh management practices. In the early 1900s mosquito control personnel constructed parallel ditches connected to the bays on many of our Atlantic coastal marshes (Smith 1907). Unfortunately, ditching occurred on many areas unnecessarily since mosquitoes do not breed in all salt marshes. Drainage of the marshes resulted in vegetational changes involving an increase in _Iva_ and _Baccharis_ bushes (Bourn and Cottam 1950). Subsequently, some observers reported on the detrimental effects of ditching (e.g. Service 1971, Daiber 1974), while others proclaimed the overall effect as beneficial (e.g. Bennett 1971, Rio 1971, Shisler 1973). The ditching on our study area, not parallel in construction, only connected mosquito breeding areas and did not markedly change the vegetation. Nevertheless, the spoil did create some slightly higher areas and Willets preferred these for nest sites.

Older gulls and terns lay larger eggs and clutches than do younger birds (e.g. Coulson 1966, 1968). The Willets nesting on the spoil piles had significantly larger eggs suggesting that they may be older, more experienced birds. This further suggests that younger birds may have been excluded from the spoil areas.

Nesting on spoil piles confers a number of advantages. Since they are the highest areas, they are drier and provide more visible areas for courtship and territorial displays. The piles provide grass cover for nest construction and concealment similar to that provided by the natural areas. Thus, spoil piles provide advantages that natural areas do not, while retaining the advantages of the natural areas.

**SUMMARY**

We examined the requirements for nesting in Willets in a salt marsh in southern New Jersey. Willets did not nest in an extensive area of tall _Spartina alterniflora_ marsh, a few nested in an area of short _S. alterniflora_, and 18 nested in a _S. alterniflora_ and _S. patens_ marsh with mosquito ditching.

The nest sites chosen by the Willets did not differ from random points with respect to several vegetation characteristics including species of vegetation, % live cover, % dead cover, mean height of live and dead grass, and distance to ecotone. Willets selected nest
sites on high ground, in this case on spoil piles. The Willets nesting in the study marshes nested closer together than expected by chance. Upon examining the dense nesting area, however, Willets nested farther apart than expected by chance. Thus, Willets spaced themselves in a clump.

We discuss the advantages of nesting on spoil piles, and the advantages and disadvantages of the nesting pattern with respect to social factors.

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Burger and Shisler • WILLET NEST SITES


DEPT. OF BIOLOGY, LIVINGSTON COLLEGE, RUTGERS UNIV., NEW BRUNSWICK, NJ 08903 AND MOSQUITO RESEARCH AND CONTROL, NEW JERSEY AGRICULTURAL EXPERIMENT STATION, NEW BRUNSWICK, 08903. ACCEPTED 1 JUNE 1977.

SYMPOSIUM ON BIRDS OF THE SEA AND SHORE

A 5-day symposium, consisting of 3 days of formal sessions and 2 days of excursions, will be held at the University of Cape Town, South Africa from 19-23 November 1979. The theme of the symposium will be “Birds of the sea and shore” and papers will be given on seabirds and waders, both inland and coastal. Excursions are planned for an offshore seabird breeding island, Langebaan Lagoon and a seawatching cruise.

Persons interested in attending the symposium should write to the Organizing Secretary, Mr. G. D. Underhill, 12 Roseberry Road, Mowbray 7700, South Africa for further information. Persons wishing to deliver a paper should also write to Mr. J. Cooper, Southern African Seabird Group, c/o FitzPatrick Institute, University of Cape Town, Rondebosch 7700, South Africa, giving details of their proposed paper.
ORGANOCHLORINE RESIDUES AND EGGSHELL THINNING IN WOOD STORKS AND ANHINGAS

HARRY M. OHLENDORF, ERWIN E. KLAAS AND T. EARL KAISER

Wood Storks (Mycteria americana) are somewhat less widely distributed today in the United States than they were in the early 1940s, and their numbers in Florida have declined to a fraction of those occurring there earlier (Ogden 1975, 1978, Palmer 1962). Populations of the Anhinga (Anhinga anhinga) have apparently remained generally stable. However, data on organochlorine residues in this species are of interest because of its close phylogenetic relationship with the Double-crested Cormorant (Phalacrocorax auritus) and Brown Pelican (Pelecanus occidentalis), 2 species in which eggshell thinning has been correlated with organochlorine residues, particularly DDE (Anderson and Hickey 1972, Blus 1970, Blus et al. 1971, 1972a, 1972b, Risebrough et al. 1971). Similar correlations have been reported in other fish-eating birds (Fox 1976, Vermeer and Reynolds 1970, Vermeer and Risebrough 1972), and Wood Storks and Anhingas are primarily fish eaters.

To determine whether either of these species might be adversely affected by environmental pollutants, we collected eggs and analyzed them for residues of organochlorines. We compared eggshell thickness of these eggs and others collected since 1946 (and now located in museum collections) with shell thickness of eggs collected before the widespread use of organochlorine pesticides.

The results reported here are part of a larger study to determine (1) geographic differences in the occurrence of environmental pollutants in Anhingas and wading birds (including herons, bitterns, ibises, and Wood Storks) in the eastern United States; (2) differences in environmental pollutant levels among those species nesting at the same localities; and (3) whether eggshell thickness had changed since the widespread use of organochlorine pesticides began in the mid-1940s.

METHODS

Wood Stork eggs were collected at the Merritt Island National Wildlife Refuge (NWR), Brevard County, Florida, in 1973. Anhinga eggs were collected at Merritt Island NWR and at 6 additional localities in 1972 and 1973: Lacassine NWR (Cameron Parish) and Atchafalaya Basin (St. Martin Parish) Louisiana; Yazoo NWR (Washington County) Mississippi; J. N. “Ding” Darling NWR (Lee County) and Payne’s Prairie (Alachua County) Florida; and Okefenokee NWR (Ware County) Georgia.

Entire clutches were collected; when the clutches consisted of 2 or more eggs, 2 eggs from each clutch were wrapped in aluminum foil and placed in plastic containers to
retard moisture loss. These eggs were refrigerated until they could be processed. Contents were then removed, placed into chemically clean jars, and then frozen pending analysis. Only 1 egg per clutch was analyzed, but shells of all eggs were saved for comparisons of eggshell thickness.

Egg volumes were measured to the nearest 1.0 ml by water displacement before the contents were removed. Residues were adjusted to fresh wet weight, assuming specific gravity of 1.0 as suggested by Stickel et al. (1973).

After the egg contents were homogenized in a mixer, a 10-g subsample was blended with sodium sulfate and extracted 7 to 8 hours with hexane in a Soxhlet apparatus. Cleanup of the extract, and separation and quantitation of pesticides and polychlorinated biphenyls (PCBs) were similar to the procedure used for the analysis of eagle carcasses (Cromartie et al. 1975). In summary, an aliquot of hexane extract equivalent to 5 g of subsample was passed through a Florisil column to remove lipids. An aliquot of this eluate was column chromatographed on silicic acid to separate the pesticides and PCBs. The organochlorines separated into 3 silicic-acid eluates were identified and quantitated by gas chromatography on a 1.83-m glass column packed with 4% SE-30/6% QF-1 on 100-120 mesh Supelcoport. PCBs were quantitated by comparing total peak area, measured by computing integrator, with that of Aroclor 1254 or 1260, whichever most closely resembled the gas chromatographic profile of the sample. Residues in 10% of the samples were confirmed with a combined gas chromatograph-mass spectrometer.

Samples were analyzed for DDE, DDD, DDT, dieldrin, mirex, heptachlor epoxide, oxychlordane, cis-chlordane (and/or trans-nonachlor), cis-nonachlor, HCB, toxaphene, endrin, and PCBs.

Recoveries of pesticides and PCBs from spiked egg tissue range from 83% to 101%. Residues in this report were not adjusted on the basis of these recoveries. Sensitivity of detection for the gas chromatograph was 0.1 ppm for pesticides and 0.5 ppm for PCBs. When PCBs were detected in trace amounts (<0.5 ppm), they were considered as 0.25 ppm for purposes of this report.

Mean organochlorine concentrations in the samples were computed on individual sample values (the residue concentration + 1) transformed to common logarithms. (After computing these values, we took their antilogs and then subtracted 1 from that value. This returned our measurements to the original units. The addition of 1 facilitated the transformation of zero values to logs.) The data were analyzed on a CDC 6400 computer using packaged subroutines from the Statistical Package for the Social Sciences (Nie et al. 1975). In some instances the presence of many zero values prevented transforming to the normal distribution, but we also calculated means of these log-transformed data (see Ohlendorf et al. 1978 for further explanation). We performed a one-way analysis of variance on the log-transformed data for DDE and PCBs to detect significant differences (P < 0.05) among the mean levels of these chemicals at the different localities for Anhingas, and among species at Merritt Island. We used the Scheffe procedure (Scheffé 1959) of multiple comparison of means to group the localities or species by mean chemical concentration into homogeneous subsets.

Eggshell thickness was measured to the nearest 0.1 mm with a modified Starrett micrometer after the shells had dried at room temperature for a least 1 month. Three measurements were taken at the "equator" of each egg and included the shell and shell membranes. Measurements were averaged to yield a single value for each egg in the clutch. Statistical testing (2-way, non-random model, analysis of variance) of eggshell thickness was based on clutch mean thickness.

For each species, eggshell thickness data were first grouped into two time periods,
Table 1

Organochlorine Residues in Wood Stork Eggs from Merritt Island National Wildlife Refuge, Florida, 1973*

<table>
<thead>
<tr>
<th>Residue</th>
<th>Number with Residues</th>
<th>Geometric Mean (ppm)</th>
<th>95% C.I.</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>DDE</strong></td>
<td>10</td>
<td>4.0</td>
<td>2.0-7.3</td>
<td>1.2-19</td>
</tr>
<tr>
<td><strong>DDD</strong></td>
<td>2</td>
<td>0.026</td>
<td>0-0.07</td>
<td>ND-0.13</td>
</tr>
<tr>
<td><strong>DDT</strong></td>
<td>3</td>
<td>0.24</td>
<td>0-0.65</td>
<td>ND-1.9</td>
</tr>
<tr>
<td><strong>Dieldrin</strong></td>
<td>2</td>
<td>0.053</td>
<td>0-1.55</td>
<td>ND-0.50</td>
</tr>
<tr>
<td><strong>Mirex</strong></td>
<td>7</td>
<td>0.30</td>
<td>0.07-0.56</td>
<td>ND-1.4</td>
</tr>
<tr>
<td><strong>Oxychlordane</strong></td>
<td>2</td>
<td>0.030</td>
<td>0-0.08</td>
<td>ND-0.20</td>
</tr>
<tr>
<td><strong>cis-chlordane</strong></td>
<td>2</td>
<td>0.032</td>
<td>0-0.08</td>
<td>ND-0.24</td>
</tr>
<tr>
<td><strong>cis-nonachlor</strong></td>
<td>1</td>
<td>0.063</td>
<td>0-0.22</td>
<td>ND-0.84</td>
</tr>
<tr>
<td><strong>HCB</strong></td>
<td>1</td>
<td>0.0045</td>
<td>0-0.01</td>
<td>ND-0.047</td>
</tr>
<tr>
<td><strong>Toxaphene</strong></td>
<td>3</td>
<td>0.059</td>
<td>0-0.15</td>
<td>ND-0.41</td>
</tr>
<tr>
<td><strong>PCBs</strong></td>
<td>10</td>
<td>1.2</td>
<td>0.7-1.9</td>
<td>0.43-3.3</td>
</tr>
</tbody>
</table>

*One egg from each of 10 clutches. Average lipid content = 5.5%. Heptachlor epoxide and endrin were not found in the samples.

1 And/or trans-nonachlor.

2 ND = not detected.

pre-1947 and 1947-1973. Data from various individual localities within time periods were subjected to analysis of variance and multiple comparisons tests before pooling into 1 region for storks and 3 for Anhingas. Localities with significant differences in mean eggshell thickness (P < 0.05) were not pooled. Differences in mean thickness between time periods were tested by individual t-tests within each region.

ORGANOCHLORINE RESIDUES

**Wood Stork.**—DDE and PCBs occurred in all 10 eggs of the Wood Stork: mirex occurred in 7 (Table 1). Eight other organochlorines were found, but they were present in fewer than half of the samples. Heptachlor epoxide and endrin were not detected.

Residue levels of DDE in Wood Stork eggs were significantly higher (P < 0.05) than residues in eggs of 9 other species sampled at Merritt Island NWR (Table 2) but not significantly different from residues in eggs of Great Blue Herons (Ardea herodias), Black-crowned Night Herons (Nycticorax nycticorax), and Cattle Egrets (Bubulcus ibis). In contrast, PCB residues in Wood Stork eggs were considerably lower than the DDE level (PCB/DDE ratio = 0.30), and there were no significant differences among species means.

**Anhinga.**—DDE and PCBs were found in 45 and 24 of the 46 Anhinga eggs analyzed; other residues occurred less frequently (Table 3). Residues of DDD, DDT, mirex, and HCB were found more frequently in samples from
Table 2
Comparison of DDE and PCB Residues (ppm, Wet Weight) in Eggs of 13 Avian Species Collected at Merritt Island National Wildlife Refuge, 1972 and 1973

<table>
<thead>
<tr>
<th>Species</th>
<th>DDE Geometric Mean</th>
<th>PCBs Geometric Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wood Stork</td>
<td>4.0 A²</td>
<td></td>
</tr>
<tr>
<td>Great Blue Heron</td>
<td>2.1 AB</td>
<td>Great Blue Heron</td>
</tr>
<tr>
<td>Black-crowned Night Heron</td>
<td>1.0 AB</td>
<td>Black-crowned Night Heron</td>
</tr>
<tr>
<td>Cattle Egret</td>
<td>0.93 AB</td>
<td>Great Egret</td>
</tr>
<tr>
<td>Great Egret</td>
<td>0.66 B</td>
<td>Wood Stork</td>
</tr>
<tr>
<td>Snowy Egret</td>
<td>0.54 B</td>
<td>Anhinga</td>
</tr>
<tr>
<td>Green Heron</td>
<td>0.49 B</td>
<td>Louisiana Heron</td>
</tr>
<tr>
<td>Louisiana Heron</td>
<td>0.49 B</td>
<td>Little Blue Heron</td>
</tr>
<tr>
<td>Little Blue Heron</td>
<td>0.41 B</td>
<td>Snowy Egret</td>
</tr>
<tr>
<td>Anhinga</td>
<td>0.39 B</td>
<td>Cattle Egret</td>
</tr>
<tr>
<td>Glossy Ibis</td>
<td>0.34 B</td>
<td>Green Heron</td>
</tr>
<tr>
<td>Least Bitter</td>
<td>0.29 B</td>
<td>White Ibis</td>
</tr>
<tr>
<td>White Ibis</td>
<td>0.27 B</td>
<td>Least Bitter</td>
</tr>
</tbody>
</table>

¹Scientific names for species not mentioned in the text are: Great Egret (Casmerodius albus), Snowy Egret (Egretta thula), Green Heron (Butorides striatus), Louisiana Heron (Hydranassa tricolor), Little Blue Heron (Florida caerulea), Glossy Ibis (Plegadis falcinellus), Least Bittern (Ixobrychus exilis), and White Ibis (Eudocimus albus).

²Within each chemical, means that share the same letter are not significantly different (P > 0.05) from each other. ND = not detected.

inland localities than in eggs from other areas. PCBs were found more commonly in the eggs from Merritt Island NWR than in those from other areas. The overall frequency of occurrence of residues (see frequency index, Table 3) was highest in the samples from inland localities. Heptachlor epoxide, cis-chlordane, cis-nonachlor, toxaphene, and endrin were not detected in the Anhinga eggs.

Among the localities, mean DDE residues were much higher in samples from Yazoo NWR and the Atchafalaya Basin than in those from other localities, and the highest DDE residue in an individual sample (15 ppm) was in an egg from the Atchafalaya Basin (Table 4). The lowest mean DDE residues were in eggs from Merritt Island, "Ding" Darling, and Okefenokee National Wildlife Refuges.

There were no differences among mean PCB residues for the various localities; means for other chemicals were not tested because the chemicals were found in less than half of the eggs. PCB/DDE ratios were below 1.0 at all localities except at Merritt Island NWR; there the PCBs were 2.8 times the level of DDE (Table 4).
TABLE 3
FREQUENCIES OF ORGANOCHLORINE RESIDUES IN ANHINGA EGGS, 1972 AND 1973*

<table>
<thead>
<tr>
<th></th>
<th>Inland¹ (N = 21)</th>
<th>Gulf Coast² (N = 15)</th>
<th>Atlantic Coast³ (N = 10)</th>
<th>Total (N = 46)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DDE</td>
<td>21 (100)</td>
<td>15 (100)</td>
<td>9 (90)</td>
<td>45 (97.8)</td>
</tr>
<tr>
<td>DDD</td>
<td>2 (9.5)</td>
<td></td>
<td>2 (4.3)</td>
<td></td>
</tr>
<tr>
<td>DDT</td>
<td>5 (23.8)</td>
<td></td>
<td>5 (10.9)</td>
<td></td>
</tr>
<tr>
<td>Dieldrin</td>
<td>1 (4.8)</td>
<td>1 (6.7)</td>
<td>2 (4.3)</td>
<td></td>
</tr>
<tr>
<td>Mirex</td>
<td>2 (9.5)</td>
<td></td>
<td>2 (4.3)</td>
<td></td>
</tr>
<tr>
<td>Oxychlordane</td>
<td>1 (4.8)</td>
<td>1 (6.7)</td>
<td>2 (4.3)</td>
<td></td>
</tr>
<tr>
<td>HCB</td>
<td>2 (9.5)</td>
<td></td>
<td>2 (4.3)</td>
<td></td>
</tr>
<tr>
<td>PCBs</td>
<td>11 (52.4)</td>
<td>6 (40)</td>
<td>7 (70)</td>
<td>21 (52.2)</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td>84</td>
</tr>
<tr>
<td>Occurrences</td>
<td>45</td>
<td>23</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>Frequency</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Index¹</td>
<td>0.165</td>
<td>0.118</td>
<td>0.123</td>
<td>0.140</td>
</tr>
</tbody>
</table>

¹ Heptachlor epoxide, cis-chlordane, cis-nonachlor, toxaphene, and endrin were not found in the samples.
² Includes Atchafalaya Basin (LA), Yazoo NWR (MS), Payne’s Prairie (FL), and Okefenokee NWR (GA).
³ Includes Lacassine NWR (LA) and Darling NWR (FL).
⁴ Includes Merritt Island NWR (FL).
⁵ Computed as: Possible occurrences = No. of clutches from that habitat (i.e. Inland, etc.) x 13 chemicals.

DDD was found only in 2 eggs from Yazoo NWR, where eggs also had the highest mean DDT level (Table 4). Mirex was found in 2 eggs from Payne’s Prairie, and HCB in 2 eggs from the Atchafalaya Basin.

EGGSHELL THICKNESS

Wood Stork.—Although mean shell thickness of eggs collected since 1946 was significantly less (-3.9%; P < 0.001) than the mean for eggs collected in Florida prior to 1947 (Table 5), eggshell thickness was not significantly correlated (P > 0.05) with any of the organochlorine residues (Table 6). However, the sample size was small, and the negative correlation of DDE and eggshell thickness approached significance (P = 0.115), meaning that eggs with higher DDE levels tended to have thinner eggshells. Correlations of eggshell thickness with most organochlorines were not tested because only DDE, PCBs, and mirex occurred in more than half of the samples.

Anhinga.—Mean shell thickness of recent eggs from Louisiana and Mississippi was significantly less (-7.5%; P < 0.05) than the mean for pre-1947
Table 4
Organochlorine Residues in Anhinga Eggs, 1972 and 1973*

<table>
<thead>
<tr>
<th></th>
<th>Number with residues</th>
<th>Residues in ppm (Wet Weight)</th>
<th></th>
<th>PCB/DDE ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>LOUISIANA:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lacassine NWR (4)</td>
<td></td>
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</tr>
<tr>
<td>DDE</td>
<td>4</td>
<td>0.79 AB</td>
<td>0.12-1.8</td>
<td>0.31-1.6</td>
</tr>
<tr>
<td>Atchafalaya Basin (10)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DDE</td>
<td>10</td>
<td>2.1 A</td>
<td>0.8-4.3</td>
<td>0.60-15</td>
</tr>
<tr>
<td>DDT</td>
<td>2</td>
<td>0.03</td>
<td>0-0.06</td>
<td>ND-0.15</td>
</tr>
<tr>
<td>Dieldrin</td>
<td>1</td>
<td>0.01</td>
<td>0-0.03</td>
<td>ND-0.09</td>
</tr>
<tr>
<td>HCB</td>
<td>2</td>
<td>0.01</td>
<td>0-0.02</td>
<td>ND-0.05</td>
</tr>
<tr>
<td>PCBs</td>
<td>3</td>
<td>0.23 A</td>
<td>0-0.56</td>
<td>ND-1.3</td>
</tr>
<tr>
<td>MISSISSIPPI</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yazoo NWR (3)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DDE</td>
<td>3</td>
<td>3.5 A</td>
<td>0.2-15</td>
<td>2.0-7.1</td>
</tr>
<tr>
<td>DDD</td>
<td>2</td>
<td>0.07</td>
<td>0-0.24</td>
<td>ND-0.13</td>
</tr>
<tr>
<td>DDT</td>
<td>3</td>
<td>0.30</td>
<td>0.07-0.59</td>
<td>0.19-0.38</td>
</tr>
<tr>
<td>PCBs</td>
<td>1</td>
<td>0.11 A</td>
<td>0-0.72</td>
<td>ND-0.36</td>
</tr>
<tr>
<td>FLORIDA:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Darling NWR (1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DDE</td>
<td>11</td>
<td>0.41 B</td>
<td>0.13-0.75</td>
<td>0.12-2.5</td>
</tr>
<tr>
<td>Dieldrin</td>
<td>1</td>
<td>0.02</td>
<td>0-0.05</td>
<td>ND-0.18</td>
</tr>
<tr>
<td>Oxychlordane</td>
<td>1</td>
<td>0.01</td>
<td>0-0.04</td>
<td>ND-0.14</td>
</tr>
<tr>
<td>PCBs</td>
<td>6</td>
<td>0.21 A</td>
<td>0.06-0.39</td>
<td>ND-0.72</td>
</tr>
<tr>
<td>Merritt Island NWR (10)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DDE</td>
<td>9</td>
<td>0.39 B</td>
<td>0.20-0.62</td>
<td>ND-0.93</td>
</tr>
<tr>
<td>PCBs</td>
<td>7</td>
<td>1.1 A</td>
<td>0.18-2.6</td>
<td>ND-6.4</td>
</tr>
<tr>
<td>Payne's Prairie (7)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DDE</td>
<td>7</td>
<td>0.76 AB</td>
<td>0.39-1.2</td>
<td>0.39-1.6</td>
</tr>
<tr>
<td>Mirex</td>
<td>2</td>
<td>0.05</td>
<td>0-0.14</td>
<td>ND-0.24</td>
</tr>
<tr>
<td>Oxychlordane</td>
<td>1</td>
<td>0.01</td>
<td>0-0.04</td>
<td>ND-0.08</td>
</tr>
<tr>
<td>PCBs</td>
<td>6</td>
<td>0.58 A</td>
<td>0-2.1</td>
<td>ND-7.2</td>
</tr>
<tr>
<td>GEORGIA:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Okefenokee NWR (1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DDE</td>
<td>1</td>
<td>0.42 AB</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>PCBs</td>
<td>1</td>
<td>0.25 A</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

* One egg from each of 46 clutches. Average lipid content = 5.6%. All eggs were analyzed for all chemicals listed in methods. Heptachlor epoxide, cis-chlordane, cis-nonachlor, toxaphene, and endrin were not found in any of the eggs.

[^1]: Number of samples collected and analyzed from that locality.

[^2]: For DDE and PCBs (considered separately), locality means that share the same letters are not significantly different from other locality means for that chemical.

[^3]: ND = not detected.
Table 5

Comparison of Wood Stork and Anhinga Mean Eggshell Thickness (mm) in 2 Time Periods

<table>
<thead>
<tr>
<th>Species</th>
<th>State(s)</th>
<th>1865–1946</th>
<th>1947–1973</th>
<th>% Change</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wood Stork</td>
<td>FL</td>
<td>93</td>
<td>0.530</td>
<td>20</td>
<td>0.483</td>
<td>-8.9</td>
</tr>
<tr>
<td></td>
<td>GA, SC</td>
<td>10</td>
<td>0.340</td>
<td>1</td>
<td>0.363</td>
<td>0.6</td>
</tr>
<tr>
<td></td>
<td>LA, MS, TX</td>
<td>6</td>
<td>0.352</td>
<td>29</td>
<td>0.326</td>
<td>-7.5</td>
</tr>
<tr>
<td>Anhinga</td>
<td>FL</td>
<td>104</td>
<td>0.343</td>
<td>45</td>
<td>0.345</td>
<td>0.6</td>
</tr>
<tr>
<td></td>
<td>GA, SC</td>
<td>10</td>
<td>0.340</td>
<td>1</td>
<td>0.363</td>
<td>0.6</td>
</tr>
<tr>
<td></td>
<td>LA, MS, TX</td>
<td>6</td>
<td>0.352</td>
<td>29</td>
<td>0.326</td>
<td>-7.5</td>
</tr>
</tbody>
</table>

1 N = number of clutches.
2 Single clutch from this time period was inadequate sample for making comparison.

eggs, but there was no significant change (P > 0.05) in shell thickness of eggs from Florida (Table 5). We did not have an adequate sample of recent eggs from Georgia and South Carolina to compare with the pre-1947 eggs from those states.

The change in clutch mean eggshell thickness was significantly correlated (P < 0.05) with the concentration of DDE in the eggs, but not with the concentration of PCBs or total organochlorines (Table 7). We did not test correlations with other chemicals because they occurred in less than half of the eggs.

Table 6

Correlation Matrix of Organochlorine Residues in Wood Stork Eggs and Change in Thickness of the Eggshells from Merritt Island National Wildlife Refuge, Florida, 1973

<table>
<thead>
<tr>
<th></th>
<th>Mirex</th>
<th>PCBs</th>
<th>Total Organochlorines</th>
<th>Clutch Mean Thickness</th>
</tr>
</thead>
<tbody>
<tr>
<td>DDE</td>
<td>0.238</td>
<td>-0.248</td>
<td>0.770***</td>
<td>-0.418*</td>
</tr>
<tr>
<td>Mirex</td>
<td>-0.055</td>
<td>0.546**</td>
<td></td>
<td>0.301</td>
</tr>
<tr>
<td>PCBs</td>
<td></td>
<td>0.079</td>
<td></td>
<td>-0.115</td>
</tr>
<tr>
<td>Total Organochlorines</td>
<td></td>
<td></td>
<td></td>
<td>-0.042</td>
</tr>
</tbody>
</table>

* N = 10 clutches.
1 Probability of correlations this high or higher as follows: * P = 0.115, ** P = 0.052, *** P < 0.005.
2 Thickness as a % of the pre-1947 mean shell thickness for Wood Stork eggs from Florida.
DISCUSSION AND CONCLUSIONS

Because we collected Wood Stork eggs at only 1 locality, we could not determine geographic patterns in this species. However, in Anhingas organochlorine residues occurred more often in eggs from inland localities than in those from coastal localities. This pattern, plus the greater frequency of PCB residues in the Anhinga eggs from Merritt Island NWR, is generally consistent with our findings in other species (Ohlendorf et al. 1974, 1978, and unpublished data).

The residues found in the Wood Stork and Anhinga eggs may not directly reflect the levels found in the nesting locality, but they probably are representative for the general area of the nesting colonies. However, Wood Storks feed as far as 125 km from their colonies while nesting and they disperse from these areas after the nesting season: birds marked in Florida have been seen in Mississippi, Alabama, Georgia, and South Carolina (J. C. Ogden, pers. comm.).

Differences in residue frequency and levels among species nesting at Merritt Island NWR (or any other particular locality) might be due to differences in diet, feeding location, or physiology of the birds, or other factors. Diets of the species we studied vary with time and place, but Great Blue Herons, Great Egrets, and night herons generally feed on larger fish of different kinds than do the other birds (Bent 1922, 1926, Palmer 1962). Night herons are particularly active at dawn and dusk, whereas the other species feed more actively during the day. Cattle Egrets and ibises feed more extensively on invertebrates. Cattle Egrets feed almost altogether in terrestrial sites whereas ibises feed largely in mud flats. Other species feed primarily in aquatic areas, eating a variety of organisms, including fish of various sizes.
Wood Storks nesting at Merritt Island feed primarily in freshwater marshes along the St. Johns River when they are nesting (J. L. Baker and J. C. Ogden, pers. comm.), but feeding locations for the other species are not known, and the various species may be exposed to different arrays of contaminants. The Wood Storks may also tend to live longer, thereby having a longer time of exposure. Physiological differences among these species are not known.

Although the differences among locality means were not statistically significant, PCB residues in eggs of most species nesting at Merritt Island NWR (including Anhingas) were usually higher than in eggs from other localities in the South (Ohlendorf et al. 1974, 1978, and unpublished data).

In our more comprehensive survey of organochlorine residues in eggs of Black-crowned Night Herons, we found mean DDE residue levels similar to those of Wood Storks only in eggs from the northeastern Atlantic coastal localities (New Jersey to Massachusetts) and from Michigan (Ohlendorf et al. 1978).

Although we found that shell thickness of Wood Stork eggs collected in Florida since 1946 was significantly less than the historical mean, there was no indication of thin-shelled egg loss or reduction in clutch size in several Florida nesting colonies that were closely studied (J. C. Ogden, pers. comm.). After the first year of our study we had found no significant change in shell thickness of Anhinga eggs from Florida (Ohlendorf et al. 1974); our final results confirm this conclusion.

**SUMMARY**

All 10 Wood Stork eggs collected at Merritt Island National Wildlife Refuge in 1973 contained residues of DDE (geometric mean 4.0 ppm wet weight) and PCBs (1.2 ppm). Nine other organochlorines were found at lower frequencies in the eggs. Eggshells from the recent period were 8.9% thinner (P < 0.001) than pre-1947 samples; decrease in eggshell thickness was more closely correlated with DDE than other organochlorines and correlation of DDE and eggshell thickness approached significance (P = 0.115).

Anhinga eggs were collected at 7 localities; 45 of the 46 eggs analyzed contained DDE residues and 21 contained PCBs. Residues of other organochlorines were found less frequently. Shell thickness of recent eggs from Louisiana and Mississippi was significantly less (-7.5%; P < 0.05) than the mean for pre-1947 eggs, but there was no significant change in shell thickness of eggs from Florida. The change in clutch mean eggshell thickness was significantly negatively correlated (P < 0.05) with the concentration of DDE in the eggs.

**ACKNOWLEDGMENTS**

We thank personnel in the following museums where oological collections were examined: American Museum of Natural History, Carnegie Museum, Charleston Museum, Clemson University, Delaware Museum of Natural History, Florida State Museum, Museum of Comparative Zoology, Ohio State University, Peabody Museum of Natural
History, Philadelphia Academy of Natural Sciences, University of Kansas, University of Massachusetts, and U.S. National Museum. In addition, we thank H. H. Harrison for allowing us to measure eggshells in his personal collection.

We appreciate the assistance of the National Wildlife Refuge staff at each of the Refuges and that of S. R. Aycock and S. A. Neshitt in collecting the samples and the individuals of the Patuxent Wildlife Research Center’s Environmental Residue Chemistry Project who took part in the chemical analyses.

K. P. Burnham, D. E. Coyne, F. R. Fieher, and G. H. Hensler wrote or modified the computer programs and provided useful suggestions relative to statistical treatment and interpretation of data. J. P. Hughes and R. D. McArthur assisted in performing the statistical analyses.

We appreciate reviews of the manuscript by J. L. Baker, J. C. Ogden, and S. N. Wiemeyer.

LITERATURE CITED


——, ———, AND ———. 1978. Environmental pollutants and eggshell thinning


HABITAT SELECTION BY BREEDING RED-WINGED BLACKBIRDS

PETER H. ALBERS

Habitat selection is a poorly understood aspect of avian behavior. Hildén (1965) proposed that landscape and vegetation initially attract birds to an area; then a detailed examination by the bird determines whether it will be used. The types of environmental stimuli used in habitat selection and their relative importance differ by species.

The Red-winged Blackbird (*Agelaius phoeniceus*) is an economically important species because it is widely distributed, very numerous, and feeds extensively on grain crops. The purpose of this paper is to describe the habitat preferences of breeding Red-winged Blackbirds in an agricultural area.

STUDY AREA AND METHODS

An area of 96.24 km² southeast of Dexter, Washtenaw County, Michigan, was used for the study. This area lies in a glacial plain of low rolling hills with small marshes and woodlots scattered throughout. Soils are primarily loams and clay loams with medium to high productivity. Roads normally follow section lines. The land is intensively cultivated for hay (grass and legumes), corn, wheat, and oats.

During the 1971 breeding season, I counted territorial male Red-winged Blackbirds in 36 randomly selected circular observation areas (100 m radius, 3.14 ha). I located these areas on an aerial photo (1:660), and I categorized them by habitat types (Table 1). I located the territory boundary by mapping the movements of territorial males. Counts were initiated on 1 May 1971 and were repeated at 10-day intervals until late July 1971 (9 time periods).

In 1972–73, I studied 25 observation areas within the 5 habitat types preferred by breeding Red-wings in 1971. Observation areas were randomly selected from the available areas within each habitat type. The limited availability of some habitats caused uneven sample sizes (Table 1). The observation areas were fields and wetlands 1 to 5 ha in size and were chosen independent of the areas used in 1971. Vegetational characteristics were used to describe each observation area and to describe each territory as a separate subunit within the observation area (Table 2; described in more detail by Albers 1975:24). Observations began in mid-March and were repeated at 14-day intervals (10 time periods). I counted females that remained in a male’s territory during the observation period as breeding females in 1972–73. Neither males nor females were marked. The selection of observation areas and the observation procedures for males were described in more detail by Albers (1976).

The density of breeding males and females was used as an indicator of their preferences for the habitat types and for the environmental factors characterizing the habitats. Preferences within a habitat type were determined by comparing the measured value of each environmental factor for the habitat type with the measured value.
### Table 1
**Habitat Types Within the Observation Areas**

<table>
<thead>
<tr>
<th>Typea</th>
<th>Description</th>
<th>Sample Sizeb</th>
</tr>
</thead>
<tbody>
<tr>
<td>Old hay</td>
<td>Grass/forb/legume fields cut at least once the previous year</td>
<td>6 7</td>
</tr>
<tr>
<td>New hay</td>
<td>Grass/forb/legume crop growing in grain fields of previous year; grain stubble visible in spring</td>
<td>4 2</td>
</tr>
<tr>
<td>Pastures</td>
<td>Grass/forb/legume fields grazed by domestic animals</td>
<td>2 2</td>
</tr>
<tr>
<td>Old fields</td>
<td>Grass/forb/legume fields not cut or planted for at least 1 year</td>
<td>7 8</td>
</tr>
<tr>
<td>Wetlands</td>
<td>Areas too wet for agricultural use</td>
<td>6 6</td>
</tr>
<tr>
<td>Cut fields</td>
<td>Grass/forb/legume fields recently cut</td>
<td></td>
</tr>
<tr>
<td>Fallow</td>
<td>Unplowed corn, wheat, oat, and soybean fields harvested the previous autumn but not seeded as in new hay</td>
<td></td>
</tr>
<tr>
<td>Woodlots</td>
<td>Stands of trees ≥ 5 m tall</td>
<td></td>
</tr>
<tr>
<td>Wheat/oats</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corn</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soybean</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Edge vegetation</td>
<td>Roadsides, field edges, fencerows, ditches</td>
<td></td>
</tr>
<tr>
<td>Human artifacts/open water</td>
<td>Roads, homes, barnyards, ponds</td>
<td></td>
</tr>
<tr>
<td>Tilled soil</td>
<td>Bare cultivated soil or fallow land periodically plowed</td>
<td></td>
</tr>
</tbody>
</table>

a All of the habitat types listed were present in the 36 observation areas of 1971.
b Number of observation areas at the beginning of the breeding season 1972–73; agricultural practices reduced the sample size of several of the habitat types during the breeding season. Table 4 shows the total area for each of these 5 habitat types.

of the same factors for the territories within the habitat type. The 20 factors used to describe the habitats (Table 2) were analyzed for each time period by simple linear regressions (SLR), stepwise multiple linear regressions (MLR), and one-way analyses of variance (ANOVA).

The 0.05 level of significance was used for all statistical tests. In the stepwise MLR, independent variables were added to the regression equation if the regression remained significant and if their inclusion improved the coefficient of determination by at least 5%.
### Table 2
Environmental Factors Used to Describe the Observation Areas

<table>
<thead>
<tr>
<th>Factor</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Observation area</td>
<td>Size in hectares</td>
</tr>
<tr>
<td>2. Males</td>
<td>Number of territorial males</td>
</tr>
<tr>
<td>3. Territory size</td>
<td>Size in hectares</td>
</tr>
<tr>
<td>4. Females</td>
<td>Number of females on a male’s territory</td>
</tr>
<tr>
<td></td>
<td>Vegetational composition of a habitat type or territory: Factors 5–13 classified into 4 categories; absent, 0–25% of vegetative cover, 26–75%, 76–100%. Old and new vegetation were treated separately.</td>
</tr>
<tr>
<td>5. Upland grasses</td>
<td></td>
</tr>
<tr>
<td>6. Alfalfa</td>
<td>Corn, wheat, oats, soybeans</td>
</tr>
<tr>
<td>7. Clover</td>
<td>Leaves ≥ 7 mm wide</td>
</tr>
<tr>
<td>8. Forbs</td>
<td>Leaves &lt; 7 mm wide</td>
</tr>
<tr>
<td>9. Crops</td>
<td></td>
</tr>
<tr>
<td>10. Broad-leaved monocots (wetland)</td>
<td>Mean of 8 readings for observation areas and mean of 4 for territories.</td>
</tr>
<tr>
<td>11. Narrow-leaved monocots (wetland)</td>
<td>Number of 10-cm sections of a circular wooden rod at least 90% obscured when placed vertically in the vegetation (after Wiens 1969).</td>
</tr>
<tr>
<td>12. Shrubs and trees &lt; 5 m</td>
<td>Number of points of contact by vegetation per 10-cm section of a circular wooden rod placed vertically in the vegetation.</td>
</tr>
<tr>
<td>13. Trees ≥ 5 m</td>
<td>Height in cm</td>
</tr>
<tr>
<td>14. Vegetational structure of a habitat type or territory:</td>
<td>Height in cm</td>
</tr>
<tr>
<td>15. Effective height</td>
<td>Habitat interface, i.e., field edges</td>
</tr>
<tr>
<td>16. Height of old vegetation</td>
<td>Three categories of fence rows; fence only, fence with grass/forb/brush/tree substrate ≥ 1 m wide, previous type with ≥ 1 tree every 25 m.</td>
</tr>
<tr>
<td>17. Height of new vegetation</td>
<td></td>
</tr>
<tr>
<td>18. Habitat edge</td>
<td></td>
</tr>
<tr>
<td>19. Fence rows</td>
<td></td>
</tr>
<tr>
<td>Presence within a habitat type or territory:</td>
<td>Three categories of trees; none, shrub/tree &lt; 5 m, tree ≥ 5 m.</td>
</tr>
<tr>
<td>20. Trees</td>
<td></td>
</tr>
</tbody>
</table>

* Factors 14 and 15 not used to describe wetland habitat.
HABITAT PREFERENCES

Males.—In 1971, the percentage of the study area represented by a habitat type each time period and the percentage of the total territorial males that were in the same habitat type each time period were compared by paired t-test (Table 3). For example, 9 percentages (9 time periods) for the amount of old hay were compared to the 9 respective percentages for the territorial males that were present in old hay. When the t-test was significant, the habitat type was considered “preferred” if the mean percentage of territorial males was greater than the mean percentage of occurrence for that habitat type and “avoided” if the percentage of territorial males was less than the mean percentage of occurrence for that habitat type. If the t-test was not significant, the habitat type was neither preferred nor avoided. All the paired t-tests were significant, therefore Red-wing males preferred old hay, new hay, pastures, old fields, and wetlands; and avoided cut fields, fallow fields, woodlots, wheat/oats, corn, soybeans, edge vegetation, human artifacts/open water, and tilled soil. All habitat types, except wetlands, received similar use during the 3 years. Most of the wetlands in the randomly located observation areas of 1971 were heavily vegetated lowlands rather than marshes with open water.

The initiation dates of territorial activity may vary slightly from year to year because of weather conditions; Fig. 1 shows the average dates for territorial activity during 1972–73. Territorial activity began in wetland and old field habitats during the 3rd week of March, followed by old hay habitat during the 1st week of April and new hay during the 3rd week of April. Livestock delayed territorial activity in pastures; activity began there between late March and late June. Male Red-wings occupied new hay and wetland habitats more rapidly than old hay and old fields. Densities of territorial males were highest 7 weeks after initiation of territorial activity in wetlands and new hay compared with 9–10 weeks in old hay and old fields.

The mean density of territorial males in each of the 5 preferred habitat types was calculated from the May–June period when territorial activity was highest (Table 4). The area within each habitat type and the numbers of breeding birds were changing during this time because of agricultural activity and seasonal changes in breeding activity (Albers 1976). The mean density for wetlands in 1971 was unusually low because most of the wetlands sampled were not of the type used by Red-wings.

Females.—Although males began territorial behavior before the females appeared, females preferred the same habitats in the same sequence as males. The time lag between territorial establishment by males and the appearance of females on territories was at least 4 weeks for pastures, 1–3 weeks for old hay, old fields, and wetlands, and zero for new hay.
## Table 3

Percentages of the Total Study Area Represented by Each Habitat Type and Percentages of the Total Territorial Males Found Within Each Habitat Type—1971

<table>
<thead>
<tr>
<th>Habitat type*</th>
<th>3 May&lt;sup&gt;a&lt;/sup&gt;</th>
<th>12 May</th>
<th>23 May</th>
<th>2 June</th>
<th>12 June</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Area (%)</td>
<td>Males</td>
<td>Area (%)</td>
<td>Males</td>
<td>Area (%)</td>
</tr>
<tr>
<td>Old hay</td>
<td>15.0</td>
<td>28.3</td>
<td>11.8</td>
<td>42.1</td>
<td>11.7</td>
</tr>
<tr>
<td>New hay</td>
<td>8.2</td>
<td>27.2</td>
<td>7.0</td>
<td>14.8</td>
<td>7.0</td>
</tr>
<tr>
<td>Pastures</td>
<td>4.2</td>
<td>5.4</td>
<td>4.2</td>
<td>9.7</td>
<td>4.2</td>
</tr>
<tr>
<td>Cut fields</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Grain</td>
<td>4.8</td>
<td>0</td>
<td>11.4</td>
<td>0</td>
<td>11.4</td>
</tr>
<tr>
<td>Corn</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Soybean</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tilled soil</td>
<td>22.1</td>
<td>0</td>
<td>24.5</td>
<td>9.0</td>
<td>9.1</td>
</tr>
<tr>
<td>Fallow</td>
<td>7.1</td>
<td>0</td>
<td>2.4</td>
<td>0</td>
<td>2.1</td>
</tr>
<tr>
<td>Old fields</td>
<td>12.3</td>
<td>28.3</td>
<td>12.5</td>
<td>22.8</td>
<td>12.5</td>
</tr>
<tr>
<td>Wetlands</td>
<td>4.0</td>
<td>10.8</td>
<td>4.0</td>
<td>8.8</td>
<td>4.0</td>
</tr>
<tr>
<td>Woodlots</td>
<td>14.1</td>
<td>0</td>
<td>14.0</td>
<td>1.8</td>
<td>14.0</td>
</tr>
<tr>
<td>Edge</td>
<td>3.1</td>
<td>0</td>
<td>3.1</td>
<td>0</td>
<td>3.8</td>
</tr>
<tr>
<td>Human artifacts</td>
<td>5.1</td>
<td>0</td>
<td>5.1</td>
<td>0</td>
<td>5.1</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>100.0</strong></td>
<td><strong>100.0</strong></td>
<td><strong>100.0</strong></td>
<td><strong>100.0</strong></td>
<td><strong>100.0</strong></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Habitat type*</th>
<th>21 June</th>
<th>2 July</th>
<th>10 July</th>
<th>20 July</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Area (%)</td>
<td>Males</td>
<td>Area (%)</td>
<td>Males</td>
<td>Area (%)</td>
</tr>
<tr>
<td>Old hay</td>
<td>4.7</td>
<td>26.7</td>
<td>2.8</td>
<td>25.0</td>
<td>2.4</td>
</tr>
<tr>
<td>New hay</td>
<td>4.1</td>
<td>11.1</td>
<td>1.9</td>
<td>8.3</td>
<td>1.8</td>
</tr>
<tr>
<td>Pastures</td>
<td>3.6</td>
<td>5.0</td>
<td>3.3</td>
<td>2.1</td>
<td>4.0</td>
</tr>
<tr>
<td>Cut fields</td>
<td>9.5</td>
<td>2.8</td>
<td>14.0</td>
<td>0</td>
<td>14.8</td>
</tr>
<tr>
<td>Grain</td>
<td>11.4</td>
<td>0</td>
<td>11.4</td>
<td>0</td>
<td>11.4</td>
</tr>
<tr>
<td>Corn</td>
<td>23.7</td>
<td>0</td>
<td>23.7</td>
<td>0</td>
<td>23.7</td>
</tr>
<tr>
<td>Soybean</td>
<td>0.2</td>
<td>0</td>
<td>0.2</td>
<td>0</td>
<td>0.2</td>
</tr>
<tr>
<td>Tilled soil</td>
<td>1.3</td>
<td>0</td>
<td>1.3</td>
<td>0</td>
<td>1.3</td>
</tr>
<tr>
<td>Fallow</td>
<td>1.0</td>
<td>0</td>
<td>1.0</td>
<td>0</td>
<td>1.0</td>
</tr>
<tr>
<td>Old fields</td>
<td>13.1</td>
<td>47.7</td>
<td>13.0</td>
<td>52.1</td>
<td>12.0</td>
</tr>
<tr>
<td>Wetlands</td>
<td>4.0</td>
<td>6.7</td>
<td>4.0</td>
<td>12.5</td>
<td>4.0</td>
</tr>
<tr>
<td>Woodlots</td>
<td>14.0</td>
<td>0</td>
<td>14.0</td>
<td>0</td>
<td>14.0</td>
</tr>
<tr>
<td>Edge</td>
<td>4.2</td>
<td>0</td>
<td>4.2</td>
<td>0</td>
<td>4.2</td>
</tr>
<tr>
<td>Human artifacts</td>
<td>5.2</td>
<td>0</td>
<td>5.2</td>
<td>0</td>
<td>5.2</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>100.0</strong></td>
<td><strong>100.0</strong></td>
<td><strong>100.0</strong></td>
<td><strong>100.0</strong></td>
<td><strong>100.0</strong></td>
</tr>
</tbody>
</table>

<sup>a</sup> Middle of time period.

<sup>*</sup> Comparison of percentages of total area and percentages of total territorial males was made by paired t-test; P < 0.05. Time periods with values of zero for area were not included in the analysis. The paired t-test was significant for every habitat type.
Fig. 1. Periods of territorial activity by male Red-winged Blackbirds and the periods when breeding females were present on the territories. The solid line indicates that territorial males and breeding females were present in both 1972 and 1973; the dotted line indicates they were present during 1 of the years.

Several females in sequence may use a male’s territory during the breeding season (Payne 1969:28, Dolbeer 1976). Therefore, the mean density of females during May and June is also only a relative measure of female breeding activity (Table 4). Females are more difficult to observe than are males; this may also have caused an underestimate of female density.

LANDSCAPE AND VEGETATIONAL CHARACTERISTICS

Vegetational composition.—A stepwise MLR analysis of male and female densities in each observation area and the vegetational components (factors 5–13, Table 2) for each habitat type in 1972–73 were inconclusive. A comparison by ANOVA of vegetation (factors 5–11) in territories and observation areas revealed that breeding Red-wings in upland habitat had slight preferences for old and new grasses (*Phleum pratense*, *Dactylis glomerata*, *Poa* spp., *Festuca* spp., *Bromus* spp.) early in the breeding season and new forbs in the middle and late season. In wetland habitat, Red-wings consistently preferred old and new broad-leafed monocotyledons (primarily *Typha* spp., and broad-leafed *Carex* spp.) and consistently rejected old and new narrow-leafed monocotyledons (primarily narrow-leafed *Carex* spp., *Phalaris arundinacea*, and *Calamagrostis canadensis*) and forbs. A detailed account of the ANOVA and MLR results may be found in Albers (1975:156–165).

Vegetational structure.—In a stepwise MLR analysis of male and female
Table 4

<table>
<thead>
<tr>
<th>Year &amp; (number of time periods)</th>
<th>Habitat type</th>
<th>Area (ha)</th>
<th>Territorial males</th>
<th>Breeding females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Males per ha (mean &amp; range)</td>
<td>Mean males</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean 71-73</td>
<td>Mean 71-73</td>
</tr>
<tr>
<td>1971(6)</td>
<td>Wetlands</td>
<td>4.5</td>
<td>2-6</td>
<td>1.05(0.45–1.11)</td>
</tr>
<tr>
<td></td>
<td>Old hay</td>
<td>5.4–17.5</td>
<td>8-26</td>
<td>1.66(0.80–1.99)</td>
</tr>
<tr>
<td></td>
<td>New hay</td>
<td>4.8–9.2</td>
<td>3-17</td>
<td>1.53(0.70–2.29)</td>
</tr>
<tr>
<td></td>
<td>Old fields</td>
<td>4.4–4.7</td>
<td>2-7</td>
<td>0.96(0.53–1.38)</td>
</tr>
<tr>
<td></td>
<td>Pastures</td>
<td>13.8–15.0</td>
<td>13-17</td>
<td>0.83(0.92–1.20)</td>
</tr>
<tr>
<td>1972(5)</td>
<td>Wetlands</td>
<td>11.2</td>
<td>34-50</td>
<td>3.78(3.03–4.46)</td>
</tr>
<tr>
<td></td>
<td>Old hay</td>
<td>7.9–23.2</td>
<td>10-25</td>
<td>1.36(0.43–2.02)</td>
</tr>
<tr>
<td></td>
<td>New hay</td>
<td>3.0–9.6</td>
<td>3-12</td>
<td>0.92(0.31–1.35)</td>
</tr>
<tr>
<td></td>
<td>Old fields</td>
<td>16.2</td>
<td>12-17</td>
<td>0.89(0.73–1.04)</td>
</tr>
<tr>
<td></td>
<td>Pastures</td>
<td>3.0–3.9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1973(4)</td>
<td>Wetlands</td>
<td>11.8</td>
<td>33-46</td>
<td>3.46(2.80–3.91)</td>
</tr>
<tr>
<td></td>
<td>Old hay</td>
<td>11.2–18.6</td>
<td>25-39</td>
<td>1.96(1.35–2.02)</td>
</tr>
<tr>
<td></td>
<td>New hay</td>
<td>2.9–6.1</td>
<td>9-11</td>
<td>2.08(1.47–3.44)</td>
</tr>
<tr>
<td></td>
<td>Old fields</td>
<td>17.7</td>
<td>14-18</td>
<td>0.95(0.79–1.02)</td>
</tr>
<tr>
<td></td>
<td>Pastures</td>
<td>3.0–5.6</td>
<td>1-5</td>
<td>0.36(0 -0.89)</td>
</tr>
</tbody>
</table>

*The combined mean for wetlands does not include 1971 because most of the wetlands sampled in 1971 were not of the type used by Red-wings.

Densities in each observation area and vegetative structure (factors 14–17, Table 2) for the combined upland habitats of 1972–73, height of new vegetation was the factor most frequently included in a significant regression; height of old vegetation and effective height were less often included, and texture was the least often included (Table 5). The inclusions of new vegetation in a significant regression occurred throughout the breeding season but all of the inclusions of old vegetation were before June. For wetland habitat, height of new vegetation was included in a significant regression twice as often as height of old vegetation.

An ANOVA comparing the vegetational structure of observation areas with the vegetational structure of territories for combined upland habitats
Table 5
Stepwise MLR Analysis of Bird Density and Vegetational Structure for Combined Upland Habitats of 1972–73

<table>
<thead>
<tr>
<th></th>
<th>Old height</th>
<th>New height</th>
<th>Effective height</th>
<th>Texture</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male density</td>
<td>3.0</td>
<td>10.0</td>
<td>2.2</td>
<td>2.1</td>
</tr>
<tr>
<td>Female density</td>
<td>4.1*</td>
<td>7.0</td>
<td>4.1</td>
<td>1.0</td>
</tr>
</tbody>
</table>

* Number of times the structural factor was included in a significant regression with bird density. Example indicates 5 instances consisting of 4 positive and 1 negative coefficients. Each factor could have been included in a maximum of 20 significant regressions over the 2 year period (10 time periods per year).

in 1972 showed that breeding Red-wings preferred areas with the tallest and densest vegetation (Table 6). Red-wings did not appear to have any preferences for texture of the vegetation. The 2 significant F-tests for old vegetative height occurred early in the breeding season, whereas significant F-tests for new vegetative height and effective height occurred throughout the breeding season. These results indicated that breeding Red-wings in upland habitats preferred the tallest old vegetation early in the breeding season, the tallest new vegetation, and the most dense vegetation.

In wetland habitat, the old vegetation was nearly always taller in territories than in observation areas, although the difference in heights was only significant in time period 1 (Table 7). The height of new vegetation was higher in territories than in observation areas during the middle of the breeding season, but none of the differences was significant. Thus, breeding Red-wings in wetland habitat appeared to have a slight preference for the tallest old vegetation.

The ANOVA of vegetational structure for 1973 was very similar to that of 1972 for old and new vegetative height and texture. The effective height of vegetation in territories was always greater than in observation areas but none of the differences was significant.

Habitat edge, fence rows, and trees.—An SLR analysis indicated significant positive correlations between male and female densities and the concentration (m per ha) of habitat edge (factor 18, Table 2) in 1972–73, primarily from March through May. An ANOVA comparing concentration of habitat edge of observation areas with that of territories revealed significantly greater concentrations of habitat edge in territories than in observation areas during March and April (Table 3). Thus, breeding Red-wings preferred areas on the periphery of fields and wetlands early in the breeding season.

A stepwise MLR analysis of the concentration of 3 types of fence rows (factor 19, Table 2) and male and female densities in 1972–73 revealed significant
negative correlations between bird density and the concentrations of all fence row types, primarily from March through mid-June. The results of ANOVA comparing concentrations of fence rows in observation areas with those of territories were inconclusive. Therefore the influence of fence rows on habitat selection by Red-wings is unclear.

All observation areas either contained trees (factor 20, Table 2) taller than 5 m or had them on the borders. Nearly all territories either contained a tree or the territory owner consistently shared a nearby tree with other territorial males.
Table 7
ANOVA Comparing the Vegetational Structure of Observation Areas With That of Territories for Wetlands—1972

<table>
<thead>
<tr>
<th>Median date time period</th>
<th>Height of old vegetation (cm)</th>
<th>Height of new vegetation (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Mean&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>21 Mar</td>
<td>5, 6</td>
<td>58.0, 79.2</td>
</tr>
<tr>
<td>1 Apr</td>
<td>4, 11</td>
<td>57.5, 68.6</td>
</tr>
<tr>
<td>16 Apr</td>
<td>6, 43</td>
<td>63.3, 73.3</td>
</tr>
<tr>
<td>1 May</td>
<td>6, 50</td>
<td>63.3, 74.3</td>
</tr>
<tr>
<td>15 May</td>
<td>6, 47</td>
<td>63.3, 74.3</td>
</tr>
<tr>
<td>29 May</td>
<td>6, 45</td>
<td>61.7, 74.2</td>
</tr>
<tr>
<td>12 Jun</td>
<td>6, 36</td>
<td>55.0, 72.2</td>
</tr>
<tr>
<td>26 Jun</td>
<td>6, 34</td>
<td>51.7, 65.6</td>
</tr>
<tr>
<td>10 Jul</td>
<td>6, 15</td>
<td>50.0, 70.7</td>
</tr>
<tr>
<td>23 Jul</td>
<td>6, 2</td>
<td>50.0, 30.0</td>
</tr>
</tbody>
</table>

<sup>a</sup> Number of observation areas, number of territories.
<sup>b</sup> Mean values for observation areas, mean value for territories.
<sup>c</sup> Level of significance, F-test; * = P ≤ 0.05.

Table 8
ANOVA Comparing the Meters of Habitat Edge per Hectare of Observation Areas With That of Territories For All Habitats Combined

<table>
<thead>
<tr>
<th>Median date time period</th>
<th>Meters of edge per hectare</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1972</td>
</tr>
<tr>
<td></td>
<td>N&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>21 Mar 14 Mar</td>
<td>22, 8</td>
</tr>
<tr>
<td>1 Apr 28 Mar</td>
<td>25, 26</td>
</tr>
<tr>
<td>16 Apr 12 Apr</td>
<td>25, 65</td>
</tr>
<tr>
<td>1 May 25 Apr</td>
<td>25, 75</td>
</tr>
<tr>
<td>15 May 9 May</td>
<td>25, 94</td>
</tr>
<tr>
<td>29 May 23 May</td>
<td>25, 97</td>
</tr>
<tr>
<td>12 Jun 6 Jun</td>
<td>21, 82</td>
</tr>
<tr>
<td>26 Jun 30 Jun</td>
<td>19, 67</td>
</tr>
<tr>
<td>10 Jul 4 Jul</td>
<td>17, 26</td>
</tr>
</tbody>
</table>

<sup>a</sup> Number of observation areas, number of territories.
<sup>b</sup> Mean value for observation areas, mean value for territories.
<sup>c</sup> Level of significance, F-test; * = P ≤ 0.05.

TERRITORY SIZE

A SLR and a stepwise MLR analysis of territory size and the landscape and vegetational characteristics (factors 5–9, 12–20, Table 2) in 1972–73 indicated that upland territory size was poorly correlated with these factors.
However, wetland territories (1) decreased in size as the proportion of broad-leafed monocots increased and as the general vegetative height increased, and (2) increased in size as the proportion of narrow-leafed monocots increased and as the general vegetative height decreased.

Territory size for the combined habitats began to increase about early May and continued until mid-June when the average territory was between 25 and 50% larger than during March (Fig. 2). The mean sizes of upland territories were usually 1.5–2.0 times larger than the mean size of wetland territories (Table 9).
Table 9  
SIZE (HECTARES) OF MALE RED-WING TERRITORIES FOR 1972–73

<table>
<thead>
<tr>
<th>Median date time period</th>
<th>Wetlands (N, Mean)</th>
<th>Old hay (N, Mean)</th>
<th>New hay (N, Mean)</th>
<th>Old fields (N, Mean)</th>
<th>Pastures (N, Mean)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1972</td>
<td>1973</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>21 Mar 14 Mar</td>
<td>7</td>
<td>0.21</td>
<td>a</td>
<td>a</td>
<td>1</td>
</tr>
<tr>
<td>1 Apr 28 Mar</td>
<td>46</td>
<td>0.17</td>
<td>2</td>
<td>0.29</td>
<td>15</td>
</tr>
<tr>
<td>16 Apr 12 Apr</td>
<td>80</td>
<td>0.15</td>
<td>8</td>
<td>0.17</td>
<td>19</td>
</tr>
<tr>
<td>1 May 25 Apr</td>
<td>91</td>
<td>0.15</td>
<td>26</td>
<td>0.37</td>
<td>8</td>
</tr>
<tr>
<td>15 May 9 May</td>
<td>93</td>
<td>0.16</td>
<td>52</td>
<td>0.40</td>
<td>18</td>
</tr>
<tr>
<td>29 May 23 May</td>
<td>89</td>
<td>0.15</td>
<td>64</td>
<td>0.36</td>
<td>23</td>
</tr>
<tr>
<td>12 Jun 6 Jun</td>
<td>76</td>
<td>0.19</td>
<td>55</td>
<td>0.35</td>
<td>16</td>
</tr>
<tr>
<td>26 Jun 20 Jun</td>
<td>67</td>
<td>0.20</td>
<td>41</td>
<td>0.30</td>
<td>13</td>
</tr>
<tr>
<td>10 Jul 4 Jul</td>
<td>38</td>
<td>0.22</td>
<td>14</td>
<td>0.35</td>
<td>a</td>
</tr>
<tr>
<td>23 Jul 18 Jul</td>
<td>8</td>
<td>0.19</td>
<td>5</td>
<td>0.26</td>
<td>a</td>
</tr>
</tbody>
</table>

* No territories.

RESPONSE TO HABITAT ALTERATION

Hay was cut between 27 May and 5 June during 1971–73. Breeding Red-wings seldom remained in their territory more than 48 h after it was cut. Red-wings did not establish territories or attempt to nest in cut fields after the vegetation grew back. The effect of hay cutting on the densities of males and females was determined by separating the habitats subject to harvest (old and new hay) from those not subject to harvest (pastures, old fields, and wetlands). Changes in male and female density were compared with the proportion of hay harvested (Fig. 3). Two relationships were apparent:

1. Densities of males and females peaked in uncut hayfields after a large amount of hay in other fields was cut. For 4 weeks after hay cutting began, 10–60% more females were in uncut hayfields than were present before hay cutting. After the 3rd week of June, the number of females in uncut hayfields decreased more rapidly than the hay was being cut. Changes in the densities of males during 1971–73 did not appear to be related to the cutting of hay, however.

2. Male and female densities in habitats not subject to cutting peaked at least 4 weeks before hay cutting began and continued to decrease during the hay harvest.

The response of breeding females to hay cutting suggests that many of the displaced females attempted to relocate their breeding effort, and that they were reluctant to use a different habitat type.
Red-winged Blackbirds in agricultural areas seem to have strong preferences for certain habitat types during the breeding season. Preferred habitats with the greatest amount of old vegetation (old fields and wetlands) are occupied early in the breeding season. Occupation of preferred habitats with inadequate vegetation is delayed until enough new vegetative growth appears (old hayfields, new hayfields, and pastures). Preferred habitat not in existence the previous year is occupied last (new hayfields). When new hayfields are finally used they are occupied very rapidly; presumably by adults without breeding sites and unsuccessful territorial males (Martin 1971:113–116, Bobolink [Dolichonyx oryzivorus] study). The selection of a particular habitat type by Red-wings may be due to site and habitat fidelity (Beer and Tibbits 1950, Nero 1956, Fankhauser 1961, Laux 1970:33–46), an ability to evaluate the quality of available areas, or a combination of fidelity and evaluation. The apparent reluctance of female Red-wings to change habitat for renesting after their hayfield habitat was cut suggests that habitat fidelity of females is very strong after the breeding effort has begun. I did not have marked females in my study, but Jackson (1971:51) reported that 21 of 25
marked females in marsh habitat renested in marshes after their nests were destroyed.

The early season preferences by Red-wings for old grasses in uplands and old broad-leafed monocots in wetlands indicate the importance of erect residual vegetation. Upland grasses and the broad-leafed monocots of wetlands are partially upright and easily visible in early spring, whereas clover, the narrow-leafed monocots of wetlands, and most forbs are not. Old alfalfa (*Medicago sativa*) was also partially upright in the early spring but it was not preferred as consistently as old grass. The initial territorial activity in the spring was early when the amount of residual vegetation was large. Structural strength of vegetation also appears to be important for nesting because female Red-wings preferred broad-leafed monocots in wetlands throughout the breeding season and new upland forbs in middle and late season.

Breeding Red-wings are attracted to tall vegetation and vegetation that restricts visibility. The height of old vegetation was important to Red-wings only in April and May. Height of new vegetation was important during the entire breeding season. Vegetation that restricted visibility was important to upland nesters, but the number of plant stems and leaves per unit area (texture) was not important by itself. Zimmerman (1971) found that male Dickcissels (*Spiza americana*) also preferred tall vegetation and vegetation that restricted visibility for their territories.

As the breeding season progresses, the relationship between breeding Red-wings and vegetation becomes less clear. Not only does vegetation change, but the gradual increase in the number of males and females (Albers 1976) indicates that territories in less preferred areas are probably being established (Svardson 1949, Zimmerman 1971). Weins (1973) reported similar temporal declines in the vegetational differences between territories and non-territorial areas for Grasshopper Sparrows (*Ammodramus savannarum*) and Savannah Sparrows (*Passerculus sandwichensis*).

If the intensity of competition among males reflects the quality of habitats, then territories in better quality habitat would be smaller as a result of the greater effort required to defend them (Fretwell 1972:104). The difference in Red-wing territory size between wetland habitat and upland habitats implies that old and new hay, old fields, and pastures are either of lower quality or are used differently than wetlands. Differences in use might occur in territorial defense, foraging, and nesting activities. Although general habitat types (upland, wetland) affect territory size, specific vegetational and landscape characteristics only appear to affect territory size in wetlands.

Several factors could account for territorial expansion in middle and late season: (1) the early use of preferred areas restricts later breeding activity
to undesirable areas, hence decreased competition and larger territories, and
(2) the abandonment of territories permits neighboring males to expand
their territories (Novy 1973). Seasonal changes in territory size have also
been reported for other grassland bird species (Wiens 1969, Martin 1971:79,

An evaluation of habitat selection by a species with a long breeding sea-
son, such as the Red-winged Blackbird, is more meaningful if it is performed
throughout the breeding season. The detectability of preferences, and per-
haps the preferences themselves, may change markedly.

SUMMARY

Habitat preferences of breeding Red-winged Blackbirds in an agricultural area were
determined by comparing population density, landscape characteristics, and vegetational
descriptions. Observations were made throughout the breeding season. Preferred breed-
ing habitats of Red-wings, in order of preference, were wetlands, hayfields, old fields,
and pastures. Males and females occupied old fields and wetlands first, then hayfields,
and finally, pastures.

Cutting of hayfields caused territorial abandonment by both sexes within 48 h. The
apparent movement of displaced females from cut hayfields to uncut hayfields suggests
that habitat fidelity of females is strong after the breeding effort has begun.

Breeding Red-wings exhibited general preferences for trees, large amounts of habitat
edge, erect old vegetation, and sturdy, tall, and dense vegetation. Vegetative forms and
species, such as upland grasses, broad- and narrow-leafed monocots in wetlands, and
forbs were important to the Red-wing at various times during the breeding season.
Landscape and vegetational preferences of breeding adults were easier to observe early
in the breeding season (March through May) than later. Vegetational growth and
increases in the size of the breeding population probably make these preferences more
difficult to detect.

Territory size was poorly correlated with landscape and vegetational characteristics
in uplands but strongly correlated with broad- and narrow-leafed monocots and vegetative
height in wetlands. Wetland territories were smaller than upland territories. Territories
increased in size during the middle and late portions of the breeding season. Habitat
selection by the Red-winged Blackbird can best be studied by evaluating vegetative
preferences throughout the breeding season.

ACKNOWLEDGMENTS

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LITERATURE CITED

ALBERS, P. H. 1975. Avian habitat selection in a region of intensive agriculture: the


GENERAL NOTES


After that time, according to Greenway (1958), successive ornithologists working there (Peters 1924, Bond 1930, Danforth 1937, V. Biaggi, a resident of several years; and A. S. Schwartz and R. W. Guth [J. Bond pers. comm.]) failed to find the wren. Pinchon (Faune des Antilles Francaises, Les Oiseaux, p. 198, Fort-de-France, 1964) the current authority, indicated that in his studies of birds of the French West Indies, he had never seen the Martinique race (T. a. martiniensis) or the Guadeloupe Wren. On 28 February 1969, M. J. C. Roché saw 3 territorial male Guadeloupe House Wrens and recorded their songs on tape near the hamlet of Cacao in northern Basse Terre (Roché pers. comm. and see also Red Data Book 2: Aves, 1966, entry for 1969). This place is about 8 km south of Ste. Rose. The apparent rarity of this race prompts me to report a second small colony of wrens which H. G. Savage and I discovered on Basse Terre in May 1973.

On 25 May 1973 we drove west 5 km along a dirt road from the Station de Recherches de Zoologie, Domaine Duclos, Petit-Bourg District. The road climbed from 150 m to 500 m at its terminus in the mountains. At lower elevations the habitat was cutover rain forest averaging 20 m in height with trees less than 1 m in diameter and with little understory. Along the final km of road the rain forest was seemingly virgin with trees up to 38 m in height and in excess of 2 m at the base. The rank understory of tree ferns and deciduous scrub in this area was broken only by a trail.

At 10:30 while standing at the beginning of the trail at the end of the road a wren sang a few meters down slope then flew to a perch in bright sunlight. We observed it with 7 × 50 binoculars for 1 min at a distance of 10 m, recognizing it as a Guadeloupe House Wren before it flew into dense brush. I taped 3 short song bouts (at 19 cm per sec with a Uher 4000 Report-L). Prior to our departure at 11:30 we saw a second wren in the company of the first.

We returned on the morning of 26 May, and found a bulldozer extending the road farther into the mountains. The spot where the wren was first observed was now leveled, but we located a pair of wrens in the general vicinity and recorded more song. On 28 May I returned to the area in the late afternoon, walked the new road to its end 350 m beyond the termination of the old road, and found 2 singing birds 150 m apart. On 29 May I searched for more wrens. Starting from the research station, I played a taped song at 1 km intervals along the road for 4 km and from that point every 100 m to the end of the old road at the 5 km mark. Two more singing males, one accompanied by a female, were found just east of the first site of observation. The two original singing males were also relocated at this time.

No additional wrens were encountered during our stay on Guadeloupe from 25 May through 1 June, even though several other locales were searched on both Basse Terre and Grand Terre. I visited an especially promising rain forest surrounding Grand Etang, a small mountain lake at 350 m on La Madeleine Mountain, about 20 km by air SSW of the area where the wrens were found. No wrens were located in 3 h of traversing the perimeter of the lake playing wren song.
Response by males to tape playback was vigorous and consisted of song, rapid flight from perch to perch, and occasional approach to within 2 m of the taperecorder. The rate of song evoked by playback, however, seemed no greater than that of wrens singing without stimulus. Each song type is uttered as many as 50 times before a different song begins.

I compared a song of the Guadeloupe House Wren with that of a House Wren (T. aedon ssp.) taped 8 April 1973 at Lake Wales, Florida. The song type of the latter consists of more syllables (30 vs 21), some of which are frequency modulated, and has a shorter intersyllabic interval (0.069 sec vs 0.024 sec) than that of the Guadeloupe House Wren (Fig. 1). To my ear the song of the Guadeloupe House Wren is the louder, richer, and more melodious of the two. Such simplification of song is seen also in West Indian populations of vireos in comparison with mainland congeners (Barlow unpubl. research).

On 26 May when male #1 was first seen, he was being chased by a Plumbeous Warbler (Dendroica plumbea). Both birds flew at each other. Then the warbler, in supplanting attack, drove the wren toward us. The encounter lasted approximately 1 min during which the wren sang loudly and the warbler gave an agitated buzzing call. The warbler cocked its tail in wren-like fashion and in general resembled wrens in behavior. Thus, in spite of substantial differences in appearance, behavioral similarities must occasionally bring the 2 species into conflict. The foraging behavior of the wrens seemed typical of that described for House Wrens (Bent, Life histories of North American nuthatches, wrens, thrashers and their allies, U.S. Natl. Mus. Bull., 195:131, 1948).

All the wrens appeared to be on territories. Female #1 was either nestbuilding or feeding nestlings. Twice she was noted carrying something in her beak as she flew into a dead bromeliad on top of the trunk of a tree fern ca. 2.5 m above the ground. I examined this site but found no nest. The male, singing loudly, followed the female as she flew about.

The small colony of wrens reported herein was separated by 8 km of rugged mountainous terrain from the 3 birds found by Roché, and I do not know if any wrens occur in the intervening area. My fruitless searches in other parts of the island suggest that this wren is at best rare and local on Guadeloupe. There are, however, probably hundreds of hectares of forest on Basse Terre comprising suitable habitat for wrens and it would be useful to know how widespread and abundant this bird is at present. A census using a tape recording for locating males should be undertaken in view of the wren’s endangered status.
I am grateful to D. W. Barr, J. A. Dick, J. D. Rising, and E. L. Rotman for constructive criticism of earlier versions of this paper. V. H. Thinl translated correspondence in French. E. L. Rotman prepared the figure and E. Harris typed the final draft. I also thank Dr. H. G. Savage, Dr. L. Gruner and the office of the Prefect of Guadeloupe for help in the field on that island. I acknowledge information concerning his earlier discovery of wrens on Guadeloupe from M. J. D. Roché. Our wrens were found incidental to studies of West Indian Vireonidae. Funds for fieldwork were provided in part from a grant to Barlow from the National Research Council of Canada.—Jon C. Barlow, Dept. of Ornithology, Royal Ontario Museum and Dept. of Zoology, Univ. of Toronto, Ontario, Canada M5S 2C6. Accepted 28 Oct. 1977.


**Pesticide levels and shell thickness of Common Loon eggs in New Hampshire.**—Eggshell thinning has been observed in many species of birds over the past 2 decades, and chlorinated hydrocarbons and PCB's have been implicated as the cause of this thinning (Ratcliffe, J. Appl. Ecol. 7:67–116, 1970; Schreiber and Risebrough, Auk 84: 119–135, 1972). Although heavy, widespread use of pesticides has probably never occurred in the Lakes Region of New Hampshire, sublethal levels of DDT, DDD, and DDE were found in salmon (*Salmo salar*), sucker (*Catostomus commersoni*), perch (*Perca flavescens*), pickerel (*Esox niger*), whitefish (*Coregonus clupeaformis*), and lake trout (*Salvelinus namaycush*) in 2 New Hampshire lakes (Seamans and Newell, N.H. Fish and Game Dept. Survey Report No. 10, 1973). The diet of the Common Loon, *Gavia immer*, consists of numerous aquatic organisms, predisposing it to accumulation of chlorinated hydrocarbons if present in the loon's food.

In this note, levels of pesticide residues (DDT, DDE, and dieldrin) and PCB's are compared with shell thickness of eggs of the Common Loon, in New Hampshire.

**Methods.**—Pesticide residue and PCB levels were measured by gas chromatography by the W.A.R.F. Institute, Madison, Wisconsin. Fourteen eggs, from 3 New Hampshire lakes were collected after they had been abandoned following disturbance or after prolonged incubation, or knocked into the water by an incubating adult. After collection, the egg contents were blown into sterilized containers, frozen, packed in dry ice, and mailed to the W.A.R.F. Institute.

Eggshell thickness was measured with a micrometer. In each egg sample, 4 different fragments were measured to the nearest 0.01 mm. Most measurements included membrane and cuticle, but in 8 cases the membrane was absent. To correct for the absence of the membrane, average membrane thickness, calculated by taking the difference between eggs with membrane and eggs without membrane \((n = 18, \bar{x} = 0.1480)\), was added to membraneless eggs \((n = 8)\).

**Results.**—Results of toxic residue analysis of 14 New Hampshire loon eggs are presented in Table 1. Average eggshell thickness of these eggs was 0.59 ± 0.05 mm. Residue levels (ppm) on a wet weight basis were: DDE = 5.88 ± 1.73; DDT = 2.44 ± 0.741; dieldrin = 0.105 ± 0.025; PCB's (total) = 24.6 ± 5.70; DDD < 0.05; and PCB's (as aroclor 1254) = 18.30 ± 4.82. Both DDT and PCB levels in New Hampshire eggs were higher than those reported by McIntyre (Ph.D. Thesis. Univ. of Minn., Minneapolis. 230 pp., 1975) in Minnesota and Saskatchewan and those reported by Vermeer (Can. Field-Nat. 87:403–408, 1973) in Alberta. Dieldrin levels were lower, however, in loon eggs from...
### Table 1

**Pesticide Residue Levels in Common Loon Eggs in New Hampshire (1975-76)**

<table>
<thead>
<tr>
<th>Lake</th>
<th>Thickness</th>
<th>DDE</th>
<th>DDT</th>
<th>Dieldrin</th>
<th>PCB's (Total)</th>
<th>DDD</th>
<th>PCB's (as arochlor 1254)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1975 Squam</td>
<td>0.53</td>
<td>7.71</td>
<td>4.58</td>
<td>—</td>
<td>43.1</td>
<td>31.9</td>
<td>&lt;0.005</td>
</tr>
<tr>
<td>1975 Squam</td>
<td>0.50</td>
<td>6.06</td>
<td>3.38</td>
<td>0.038</td>
<td>31.9</td>
<td>7.8</td>
<td>&lt;0.005</td>
</tr>
<tr>
<td>1975 Winn.</td>
<td>0.50</td>
<td>28.5</td>
<td>8.19</td>
<td>0.13</td>
<td>67.9</td>
<td>1.0</td>
<td>1.1</td>
</tr>
<tr>
<td>1975 Squam</td>
<td>0.62</td>
<td>3.0</td>
<td>0.30</td>
<td>0.06</td>
<td>2.9</td>
<td>0.19</td>
<td></td>
</tr>
<tr>
<td>1975 Squam</td>
<td>0.58</td>
<td>3.9</td>
<td>1.3</td>
<td>0.06</td>
<td>17.2</td>
<td>0.56</td>
<td></td>
</tr>
<tr>
<td>1975 Squam</td>
<td>0.62</td>
<td>3.8</td>
<td>2.1</td>
<td>0.13</td>
<td>60.6</td>
<td>1.1</td>
<td></td>
</tr>
<tr>
<td>1976 Squam</td>
<td>0.55</td>
<td>5.6</td>
<td>2.6</td>
<td>0.20</td>
<td>36.5</td>
<td>&lt;0.05</td>
<td>29.5</td>
</tr>
<tr>
<td>1976 Wicwas</td>
<td>0.60</td>
<td>5.9</td>
<td>4.7</td>
<td>0.31</td>
<td>56.8</td>
<td>&lt;0.05</td>
<td>46.4</td>
</tr>
<tr>
<td>1976 Squam</td>
<td>0.60</td>
<td>4.7</td>
<td>0.98</td>
<td>0.20</td>
<td>10.2</td>
<td>&lt;0.05</td>
<td>7.3</td>
</tr>
<tr>
<td>1976 Squam</td>
<td>0.67</td>
<td>3.9</td>
<td>0.94</td>
<td>0.11</td>
<td>10.4</td>
<td>&lt;0.05</td>
<td>7.5</td>
</tr>
<tr>
<td>1976 Squam</td>
<td>0.64</td>
<td>4.6</td>
<td>1.8</td>
<td>0.23</td>
<td>19.7</td>
<td>&lt;0.05</td>
<td>15.5</td>
</tr>
<tr>
<td>1976 Squam</td>
<td>0.55</td>
<td>7.8</td>
<td>3.7</td>
<td>0.25</td>
<td>37.6</td>
<td>&lt;0.05</td>
<td>29.3</td>
</tr>
<tr>
<td>1976 Winn.</td>
<td>0.64</td>
<td>5.6</td>
<td>2.1</td>
<td>0.20</td>
<td>22.3</td>
<td>&lt;0.05</td>
<td>16.5</td>
</tr>
<tr>
<td>1976 Winn.</td>
<td>0.61</td>
<td>8.1</td>
<td>2.6</td>
<td>0.07</td>
<td>30.7</td>
<td>&lt;0.05</td>
<td>22.4</td>
</tr>
</tbody>
</table>

\[ \bar{x} = 0.59, \text{SD} = \pm 0.05 \]

*Residue levels given as ppm, wet weight basis (x = geo. mean ± S.E.).
Thickness with membrane, mm.
Only 8 eggs of 1976 were analyzed for PCB's as arochlor 1254. This represents a refinement of laboratory technique in 1976.
Lake Winnipauske.
Table 2
Pesticide Residue Levels of Common Loon Eggs in Various Regions of North America

<table>
<thead>
<tr>
<th>Locality</th>
<th>N</th>
<th>DDE</th>
<th>DDD</th>
<th>DDT</th>
<th>Dieldrin</th>
<th>PCB's (as arachlor 1254)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>North Central Minnesota</td>
<td>9</td>
<td>4.99 ± 0.8</td>
<td>1.28</td>
<td>0.51</td>
<td>0.29</td>
<td>12.7 ± 1.2</td>
<td>McIntyre (1975)</td>
</tr>
<tr>
<td>New Hampshire</td>
<td>3</td>
<td>4.76 ± 0.14</td>
<td>NC²</td>
<td>0.17</td>
<td>0.26</td>
<td>20.39 ± 12.4</td>
<td>McIntyre (1975)</td>
</tr>
<tr>
<td>Saskatchewan</td>
<td>7</td>
<td>6.28 ± 1.6</td>
<td>NC</td>
<td>0.99</td>
<td>1.40</td>
<td>14.7 ± 1.7</td>
<td>McIntyre (1975)</td>
</tr>
<tr>
<td>Alberta</td>
<td>15</td>
<td>1.7 ± 0.01</td>
<td></td>
<td></td>
<td></td>
<td>1.2 ± 0.4</td>
<td>Vermeer (1973)</td>
</tr>
<tr>
<td>New Hampshire</td>
<td>14</td>
<td>5.88 ± 1.73</td>
<td>TR³</td>
<td>2.44 ± 0.74</td>
<td>0.105 ± 0.025</td>
<td>18.30 ± 4.82</td>
<td>This study</td>
</tr>
</tbody>
</table>

¹ All values given in ppm. wet weight (x = geo. mean ± S.E.).
² Not checked.
³ Trace.

Summary.—During 1975 and 1976, 51 eggs of the Common Loon, Gavia immer, in New Hampshire were measured for thickness (x = 0.58 ± 0.01 mm). Fourteen of these eggs, from 3 lakes, were analyzed for pesticide residue (DDT, DDD, DDE, and dieldrin), and PCB (polychlorinated biphenyl) levels. Significant correlations (P < 0.05) were found

Table 3
Thickness of Eggshells of the Common Loon in Various Parts of North America

<table>
<thead>
<tr>
<th>Locality</th>
<th>Dates Collected</th>
<th>N</th>
<th>x (mm) ± S.E.</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minn.</td>
<td>1970–74</td>
<td>55</td>
<td>0.55 ± 0.01</td>
<td>McIntyre (1975)</td>
</tr>
<tr>
<td>Me., N.H.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N.Y., N.S.</td>
<td>museum specimens</td>
<td>38</td>
<td>0.65 ± 0.01</td>
<td>Anderson et al. (1970)</td>
</tr>
<tr>
<td>Lab., Nfld.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alberta</td>
<td>1972</td>
<td>15</td>
<td>0.57 ± 0.01</td>
<td>Vermeer (1973)</td>
</tr>
<tr>
<td>N.H.</td>
<td>1975–76</td>
<td>51</td>
<td>0.58 ± 0.01</td>
<td>This study</td>
</tr>
<tr>
<td>Hatched (N.H.)</td>
<td>1975–76</td>
<td>10</td>
<td>0.60 ± 0.01</td>
<td>This study</td>
</tr>
<tr>
<td>Infertile or Deserted (N.H.)</td>
<td>1975–76</td>
<td>9</td>
<td>0.55 ± 0.02</td>
<td>This study</td>
</tr>
</tbody>
</table>
between eggshell thickness and DDT and DDE residue levels. Little significant difference in eggshell thickness was found between successful and nonsuccessful eggs.

Acknowledgments.—This study was conducted under the auspices of the Loon Preservation Committee of the Audubon Society of New Hampshire. I thank Ralph Kirshner and Geoff LeBaron for aid in collecting eggs. David Hammond and Rawson Wood provided valuable suggestions regarding interpretation of data. Brian Harrington offered help in statistical interpretation. I also thank Peter Stettenheim for critical review and Fred Lindzey for editing and numerous helpful suggestions.—SCOTT A. SUTCLIFFE, Institute of Natural and Environmental Resources, Petee Hall, Univ. of New Hampshire, Durham 03824. Accepted 13 Sept. 1977.


Declines in environmental pollutants in Olivaceous Cormorant eggs from Texas, 1970–1977.—Changes induced by environmental pollutants in bird eggs have been reported for many species. Egg residues and shell thickness changes have been especially noted in fish-eating birds and the use of aquatic species as “indicators” of levels of pollutants in the environment has been proposed (Moore, J. Appl. Ecol., Suppl., 3:261–269, 1966). In this study we report changes in residue levels and shell thickness of Olivaceous Cormorant (Phalacrocorax olivaceus) eggs collected in Texas during the 1970’s.

Sidney Island, a National Audubon Society sanctuary located in Sabine Lake, Texas, was the study area. In 1976 and 1977 we collected abandoned cormorant eggs after they were blown or knocked from nests. Eggs were washed and allowed to air dry before measuring. Five measurements were made from around the blowhole of intact eggs (shell plus membrane) or around the “equator” of broken eggs using a Starrett 1010 M micrometer calibrated to 0.01 mm. We also measured museum specimens collected along the Texas-Louisiana coast prior to 1940. Contents of individual eggs from different nests collected in 1976 (n = 2) and 1977 (n = 5) were analyzed for chlorinated hydrocarbons and polychlorinated biphenyls (PCBs) by the Agricultural Analytical Services Dept., Texas Agricultural Experiment Station, Texas A&M University according to established United States Department of Agriculture procedures (Pesticide Analytical Manual, United States Dept. Health, Education, and Welfare, Food and Drug Admin., Vol. 1, Sec. 212.13, 1968). Residue analysis was performed by gas chromatography using electron capture detection on a Hewlett-Packard 5700 series gas chromatograph. All analyses were performed on 2 columns for confirmation of results. Results of 1976 and 1977 residue and thickness analyses were combined due to similarity of results. To determine temporal changes in shell thickness and residue levels in Texas populations of Olivaceous Cormorants during the 1970’s, our results were compared with data obtained in a similar manner by K. A. King (pers. comm., U.S. Fish and Wildl. Ser., Patuxent Wildl. Res. Center, Gulf Coast Field Station, Victoria, TX, 1977). All further reference to “1970 results” will mean this study.

All residues in 1976–77 samples were significantly lower than levels in 1970 eggs (Table 1). Zitko (Bull. Environ. Contam. Toxicol. 16:399–405, 1976) found that most reports from 1964 to 1971 indicated that levels of DDE, dieldrin, and PCBs reached a maximum around 1970 and are now either decreasing or remaining constant. DDE residues in Brown Pelican (Pelecanus occidentalis) eggs from Texas declined from 3.2
Table 1

Residues in Olivaceous Cormorant Eggs in Texas

<table>
<thead>
<tr>
<th>Residue</th>
<th>1970 (n = 5)</th>
<th>1976–77 (n = 7)</th>
<th>% Change</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( \bar{x} )</td>
<td>S.E. (%)</td>
<td>( \bar{x} )</td>
</tr>
<tr>
<td>p, p'-DDE</td>
<td>6.22</td>
<td>2.08 100</td>
<td>0.400</td>
</tr>
<tr>
<td>Dieldrin</td>
<td>0.30</td>
<td>— 20' 100</td>
<td>0.018</td>
</tr>
<tr>
<td>PCB^2</td>
<td>32.00</td>
<td>5.83 100</td>
<td>1.890</td>
</tr>
<tr>
<td>Heptachlor Epoxide^3</td>
<td>0.032</td>
<td>0.016 100</td>
<td>—</td>
</tr>
</tbody>
</table>

1 Values represent residues on a wet-weight basis.
2 Arochlor 1254 and 1260.
3 This residue was separated from PCBs in 1977 eggs only.
4 Dieldrin found in detectable levels in only 1 egg in 1970 (1970 \( \bar{x} \) for dieldrin, all eggs = 0.06 ± 0.134, -70%; \( p > 0.05 \)).
* \( p < 0.05 \), ** \( p < 0.01 \), t-test.


Comparisons of 1970 and 1976–77 eggshell measurements with those of pre-1940 ("pre-DDT era") eggs revealed little difference in thickness (Table 2). Most authors agree that a 10–20% change in shell thickness is needed before reproductive failures are indicated (Faber and Hickey, Pestic. Monit. J. 7:27–36, 1973). Cormorant eggshell thickness was apparently not affected by residues in the 1970's in Texas.

Since the greatest use of chlorinated hydrocarbon pesticides in the United States was in the early 1960's (Ware, Pesticides, W. H. Freeman and Co., San Francisco, 1975), aquatic birds may have been affected by environmental contaminants during those years. We were unable to obtain eggshells collected from coastal Texas during the 1950's and 1960's. Breeding populations of Olivaceous Cormorants in Texas reached a recorded low in the early 1960's, but have been steadily increasing since about 1967 (Morrison and Slack, Am. Birds, 31:954–959, 1977). DDE residues in Olivaceous Cormorant eggs during the 1970's apparently did not adversely affect reproduction. The role that environmental pollutants played in the population levels of Olivaceous Cormorants prior to 1970 must remain speculative. However, current residues do not appear to be adversely affecting Olivaceous Cormorant populations in Texas.

Table 2

Shell Thickness of Olivaceous Cormorant Eggs in Texas (mm)

<table>
<thead>
<tr>
<th>Date</th>
<th>n (eggs)</th>
<th>( \bar{x} )</th>
<th>S.E.</th>
<th>% Change from Pre-1940</th>
<th>1970</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-1940</td>
<td>75</td>
<td>0.328</td>
<td>0.004</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>1970</td>
<td>24</td>
<td>0.323</td>
<td>0.006</td>
<td>-1.5</td>
<td>—</td>
</tr>
<tr>
<td>1976–77</td>
<td>21</td>
<td>0.341</td>
<td>0.004</td>
<td>+4.0*</td>
<td>+5.5*</td>
</tr>
</tbody>
</table>

* \( p < 0.05 \), t-test.
We thank K. A. King for assistance in design of the study and preparation of the manuscript. A. R. Hanks and Linda Bynum, Pesticide Section, Agricultural Analytical Services Dept., Texas Agricultural Experiment Station, Texas A&M Univ., performed residue analysis and assisted in data interpretation. We appreciate critical reviews of the manuscript by L. F. Kiff, N. J. Silvy, E. G. Bolen, E. E. Klaas, and G. A. Fox. We acknowledge the cooperation of personnel at the following locations where oological records and collections were examined: Western Foundation of Vertebrate Zoology; San Bernardino County Museum (E. Cardiff, Curator); and the Dept. of Zoology, Clemson Univ. (P. B. Hamel). This study was supported by a Research Fellowship awarded to MLM by the Rob and Bessie Welder Wildlife Foundation, Sinton, Texas.—Michael L. Morrison, R. Douglas Slack, and Edwin Shanley, Jr., Dept. of Wildlife and Fisheries Sciences, Texas A&M Univ., College Station 77843. Accepted 10 Oct. 1977.


Turkey Vulture eggshell thinning in California, Florida, and Texas.—The Turkey Vulture (Cathartes aura) seems to be declining in numbers in parts of North America (Arbib, Am. Birds 25:948-949, 1971; Russell, Auk 90:877-887, 1973), but neither the magnitude of the change nor its causes have been documented. Eggshell thinning has been demonstrated in 54 species of birds of 10 taxonomic orders; at least some thinning has been caused by chemical pesticides, particularly p,p'-DDE. Thinning of 20% or more has been suggested to result in reproductive failure and population decline (Stickel, pp. 25-74 in Ecological Toxicology Research, A. D. McIntyre and C. F. Mills, eds., Plenum Publ. Corp., New York, 1975). I examined Turkey Vulture eggshells from California, Florida, and Texas to see if significant thinning had occurred in various populations of this species.

The 76 sets of Turkey Vulture eggs examined were from the collection of the Western Foundation of Vertebrate Zoology in Los Angeles. Thirty-nine were from west-central California, 21 were from central Florida near Orlando, and 16 sets were from Texas. Sets were divided into 2 groups: those collected prior to 1947 (the pre-DDT period) and those collected since 1947 (Table 1).

Blown eggs were weighed to the nearest 0.001 g in a Mettler Top Loading Balance (Model P120), and length and breadth were measured to the nearest 0.01 mm with a dial vernier caliper. A “thickness index” (Ratcliffe, Nature 215:208-210, 1967) was calculated for each egg, and a mean thickness index was computed for the eggs from each geographic area and each time period.

Significant differences (P < 0.05, t-test comparison) existed between pre-1947 and post-1947 samples from all areas (Table 1). Florida eggs were somewhat lighter in weight than California eggs during both periods, but the percentage decrease after 1947 was similar in both areas. The Texas sample showed an even greater reduction. However, the sample size is small and may be biased by local environmental factors: the pre-1947 eggs were all taken from northern Texas and most of the later eggs were from the Texas lowlands. Texas eggs for both time periods averaged lighter in weight than either Florida or California eggs. I contacted several other museums for Turkey Vulture eggs to increase the sample size, but no other Texas specimens from appropriate areas could be located.

The 11-12% thinning in eggs from California and Florida is not of the magnitude
Measurements of Turkey Vulture Eggshells

<table>
<thead>
<tr>
<th>State</th>
<th>Year</th>
<th>Sample size (eggs)</th>
<th>Mean shell weight (g)</th>
<th>Mean thickness index¹</th>
<th>Percent change</th>
</tr>
</thead>
<tbody>
<tr>
<td>California</td>
<td>Pre-1947</td>
<td>39</td>
<td>7.60 ± .096²</td>
<td>2.25 ± .075</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1947+</td>
<td>36</td>
<td>6.72 ± .112</td>
<td>2.00 ± .102</td>
<td>-11*</td>
</tr>
<tr>
<td>Florida</td>
<td>Pre-1947</td>
<td>20</td>
<td>7.28 ± .162</td>
<td>2.09 ± .023</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1947+</td>
<td>22</td>
<td>6.22 ± .197</td>
<td>1.84 ± .043</td>
<td>-12*</td>
</tr>
<tr>
<td>Texas</td>
<td>Pre-1947</td>
<td>16</td>
<td>7.19 ± .187</td>
<td>2.10 ± .043</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1947+</td>
<td>16</td>
<td>5.76 ± .201</td>
<td>1.73 ± .063</td>
<td>-18*</td>
</tr>
</tbody>
</table>

¹ Weight (mg)/length (mm) × breadth (mm).
² ± standard error.
³ Differences significant at P < 0.05; means compared using the t-test.

generally associated with declines in productivity. If the Texas data are representative of Turkey Vultures there, then the reproductive capabilities of that population may be affected. Field studies of the breeding success of the Turkey Vulture in Texas would appear especially appropriate at this time.

I thank Lloyd Kiff and Clark Sumida, Western Foundation of Vertebrate Zoology, for assistance with eggshell measurements.—SANFORD R. WILBUR, U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Ojai, CA 93023. Accepted 30 Sept. 1977.


An experimental analysis of the interrelationship between nest density and predation in old-field habitats.—The relationship between nest density and intensity of predation has been found to be positive in most of the studies dealing with species nesting in marsh environments (Tinbergen et al., Behaviour 28:307–321, 1967; Goransson et al., Oikos 26:117–120, 1975). Some authors have presented evidence which suggests that this relationship may also apply to avian communities in upland habitats (Krebs, Ecology 52:2–22, 1971; Fretwell, Populations in a Seasonal Environment, Princeton Univ. Press, Princeton, NJ, 1972). Unfortunately no experimental studies have tested this hypothesis. This study was aimed at answering the question: Does the spatial distribution of nests influence their predation rates in old-field habitats?

Study areas and methods.—The experiment was performed from May through July 1976 at Miami University’s field station on the Bachelor Estate approximately 2 km west of Oxford, Butler County, Ohio. A full description of the study area can be found in Gottfried and Thompson (Auk 95:304–312, 1978). Two 4-ha areas were used during the experiment. In Area A the experimental nests were densely distributed (12.7/nests), while in Area B the experimental nests were more dispersed (4.7 nests/ha), simulating normal
nest density. Both nonadjacent areas were similar in habitat, number of avian species, and number of predators present.

The experimental design was as follows: I placed abandoned nests of American Robins (Turdus migratorius), Cardinals (Cardinalis cardinalis), and Field Sparrows (Spizella pusilla), each containing 2 eggs of the Japanese Quail (Coturnix coturnix), in nest sites that appeared typical of those used by the first 3 aforementioned species. Sixteen such nests (8 in Area A and 8 in Area B) were set out on the Sunday of each of 9 weeks, beginning on 9 May 1976; from these, 8 were selected (4 in each area) by lot to visit daily. I visited these 8 nests in the late afternoon or early evening but did not inspect the remaining 8 nests until Saturday. On that day (day 6 of exposure) I collected and removed any eggs that remained in the 16 nests. On Sunday, I moved all nests to different locations, added fresh quail eggs, and repeated the procedure. Thus, during the 8 weeks I placed the experimental nests at 144 different locations.

Dispersion of the experimental nests was achieved by first establishing a grid of 16 evenly spaced points in each area, then using alternate points for placement of each week's 8 nests. The distance between the points in Area A was 15 m, while in Area B they were 40 m apart. The actual location of each nest in relation to the point was determined by selecting 2 numbers between 0 and 18 from a table of random numbers. These numbers dictated the distance in paces and compass direction from the point (even, north and east; odd, south and west) that each nest was to be placed. The nest was then placed in the nearest site that appeared suitable.

Upon finding an experimental nest with 1 or both eggs missing, I examined the nest and ground below to determine if wind had dumped the contents. If so, the nest was excluded from all analyses.

Predation rates.—The numbers of nests predated in Area A (dense nests) and Area B (non-dense nests) were compared to determine if nest density influences the probability of nest detection by predators (Table 1). Overall, a slightly greater number of nests in Area A were predated (31% of Area A nests, 24% of Area B nests), but these differences are not significantly different ($\chi^2 = 0.59, p > 0.05, 1 \text{ d.f.}$). Monthly comparisons of the nest predation in both areas are also not significantly different (May $\chi^2 = 1.37, p > 0.05$; June $\chi^2 = 1.51, p > 0.05$; July $\chi^2 = 1.74, p > 0.05$).

Daily nest visitation did not increase the predation rate. In Area A (dense nest distribution) 28% of the visited and 34% of the unvisited nests were predated ($\chi^2 = 0.11, p > 0.05, 1 \text{ d.f.}$), while in Area B (non-dense nest distribution) 23% of the visited and 24% of the unvisited nests were predated ($\chi^2 = 0.03, p > 0.05, 1 \text{ d.f.}$).

Nest survival.—The day of nest predation was analyzed for each visited nest to determine if the length of the survival period was influenced by the spatial distribution of nests. Although the predated densely dispersed nests in Area A survived a slightly greater length of time, the differences are not significant (Mann-Whitney $U = 55.5, p > 0.05$). Small sample sizes preclude a monthly comparison of nest survival.

Discussion.—These experiments do not support the hypothesis that the spatial distribution of nests in upland-old-field habitats influences their probability of being predated. Why should the distribution of nests influence the predation rate of experimental nests in marsh environments and not in upland-old-field habitats? There may be at least 2 major reasons for this dichotomy. First, many species (e.g. gulls and terns) nesting in marsh habitats are primarily colonial nesters which have adopted this strategy as a defense against predators. Yet predators are drawn to these areas and do take a large toll on the eggs and young (Patterson, Ibis 107:433-459, 1965). Thus, predators in these habitats could be expected to take a greater advantage of increased nest density, than
Table 1
The Outcome of Densely and Non-Densely Distributed Experimental Nests, According to Month

<table>
<thead>
<tr>
<th>Month</th>
<th>Densely Distributed Nests</th>
<th>Non-Densely Distributed Nests</th>
<th>Destroyed by Weather</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pred.*</td>
<td>Succ.**</td>
<td>Pred.</td>
<td>Succ.</td>
</tr>
<tr>
<td>May</td>
<td>Visited nests</td>
<td>8</td>
<td>33</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Unvisited nests</td>
<td>8</td>
<td>33</td>
<td>3</td>
</tr>
<tr>
<td>June</td>
<td>Visited nests</td>
<td>1</td>
<td>4</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Unvisited nests</td>
<td>1</td>
<td>4</td>
<td>11</td>
</tr>
<tr>
<td>July</td>
<td>Visited nests</td>
<td>1</td>
<td>4</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Unvisited nests</td>
<td>2</td>
<td>8</td>
<td>7</td>
</tr>
<tr>
<td>Total</td>
<td>21</td>
<td>15</td>
<td>47</td>
<td>33</td>
</tr>
</tbody>
</table>

* Predated nests.
** Successful nests = no quail eggs missing.

would their counterparts in old-field habitats, where colonial nesting is rare. The densities of breeding bird populations in these upland habitats are buffered to a greater degree by territorial behavior (Brown, Wilson Bull. 81:293–329, 1969), and thus never reach the densities of marsh dwelling species.

The type of predator may also have some bearing on the hypothesis. There is evidence to suggest that the 2 environments may be affected by different types of predators. In marsh environments where colonial nesters predominate, sight-oriented avian and mammalian predators appear to cause most of the losses (Hammond and Foreward, J. Wildl. Manage. 20:243–247, 1956; Tinbergen et al., op. cit.; Dwernychuk and Boag, J. Wildl. Manage. 36:955–958, 1972; Picozzi, J. Wildl. Manage. 39:151–155, 1975). In old-field habitats, snakes appear to be the major predator, although birds may cause minor losses (Gottfried and Thompson, Auk op. cit.). A visual predator will usually capitalize on the opportunities afforded by a newly found nest by continuing to search in the immediate area for additional nests (Tinbergen et al., op. cit.). A snake, on the other hand, will often return to its burrow and, only after a period of time resume, its hunting activities, thus sacrificing any gains accrued by finding a nest (Goin and Goin, Introduction to Herpetology, W. H. Freeman and Co., San Francisco, 1971).

Fretwell (1972) hypothesized the positive relationship between nest density and predation pressure on the basis of woodland data where the Blue Jay (Cyanocitta cristata) is a primary predator of nests. Blue Jays appear to be adept at finding nests by visual cues and would thus be able to exploit a community where nests are densely distributed. It should also be noted that Fretwell's studies were made with nesting birds
and thus took into account the presence of parental and nestling activity in and around the nest. It can thus be argued that the use of experimental nests biased the results in the present study. However, Gottfried and Thompson (Auk op. cit.) found that the predation rate of experimental and natural nests were not significantly different (i.e. the presence of parental activity around the nest did not increase the rate of predation). It would thus appear that no sweeping generalizations can be made on the relationship between nest density and predator pressure in upland habitats, as the type of predator may differ from habitat to habitat.

I benefited from discussions with Dr. Charles Thompson. I also wish to thank P. Caprio for supplying the quail eggs.—BRADLEY M. GOTTFRIED, Dept. of Zoology, Miami Univ., Oxford, OH 45056. (Present address: Dept. of Biology, College of St. Catherine, St. Paul, MN 55105).


**Canada Goose takes over Mallard nest.—**Waterfowl are attracted to the park ponds in Allentown, Pennsylvania due to the great amount of artificial food supplied by park visitors. Mallards (*Anas platyrhynchos*) and Canada Geese (*Branta canadensis*) often nest very close to one another in the urban and suburban parks. This tendency may be a response to the limited amount of suitable nesting habitat in the park areas. Frequently I have found nests much closer together and the over-all nesting density greater than that reported by Drewien (Wilson Bull. 82:95–96, 1970). On 1 April 1977, I located a wild Mallard nest with 11 eggs and a wild Canada Goose nest with 6 eggs on a small, 0.15 ha island, in one of the park ponds. The nests were 1.2 m apart and both hens were incubating. Periodic checks of each nest revealed a loss of 4 eggs from the Mallard nest on 13 April, the result of some unknown predator. There was no change in the number of Canada Goose eggs during the period.

On 20 April, during a regular nest check, I observed 1 Canada Goose egg in the Mallard nest and 1 egg missing from the goose nest. Because of the inaccessibility of the pond and island to the public, I concluded that the goose egg rolled from the Canada Goose nest, possibly when the female was turning the eggs, and the nearby Mallard hen retrieved the loose egg. Many ground nesting birds are known to exhibit such egg retrieving behavior. The Mallard hen then continued incubating her 7 original eggs, and the goose egg, while the Canada Goose remained on her own nest, minus 1 egg. The Canada Goose did not lay another egg; she was 18 days into the incubation period.

On 23 April, the female Canada Goose was observed sitting on the Mallard nest that contained its egg, defending it from the Mallard hen, which continually made attempts to get back on her own nest. Later that same day, 5 Mallards hatched from beneath the incubating Canada Goose. The 1 goose egg and 2 Mallard eggs did not hatch. The Mallard hen continued attempting to reclaim her nest, but the female Canada Goose became very defensive, tearing feathers from the duck’s breast and neck.

The next day, 24 April, a Mallard hen was observed with a brood of 5 ducklings on the pond, and the female Canada Goose had returned to her original nest, after neglecting it for over 12 h. All 5 remaining goose eggs hatched on 30 April. The 1 goose egg that remained in the Mallard nest did not hatch.
Later observations on brood success revealed a loss of 4 Mallard ducklings by 28 April. The remaining duckling apparently survived as did the 5 juvenile Canada Geese.

I would like to thank Allentown’s Urban Observatory Board for their permission to publish these findings. I also thank my co-worker, Terry L. Master, as well as Dr. Carl Oplinger and Dr. John Trainer for the helpful suggestions and criticism in preparing this note.—THOMAS N. MATHER, Dept. of Entomology and Applied Ecology, Univ. of Delaware, Newark, DE 19711. Accepted 24 Feb. 1978.


Notes on food habits of the Plain Chachalaca from the Lower Rio Grande Valley.—The Plain Chachalaca (Ortalis vetula) is an endemic species of the brushy resacas in the delta of the Lower Rio Grande Valley, Texas. The food habits, habitats, and status of this bird have been recently examined by Marion (1974, Wilson Bull, 86: 200–205; 1975, Texas Parks Wildl. 33:16–18; 1976, Auk 93:376–379). This study provides additional information on the food habits of the Plain Chachalaca in south Texas.

Nineteen Plain Chachalacas were collected by shooting in late December, 1976 from near San Benito, Cameron Co., Texas. On necropsy, esophageal and gizzard contents were stored in 70% ethyl alcohol for later study. A reference herbarium collection of plants was made in areas from which birds were collected. Fruits and leaves from upper digestive tract contents were compared grossly with representative plant species from the region. Also, a microscopic technique for identifying plants from the fruit and leaf epidermal cell structure was employed (Sparks and Malechek, 1968, J. Range Manage. 21:264–265). Plants were identified to species where possible, but in the case of several species of composites and other families only identification to genus was possible. Likewise, where only trace amounts of material occurred even generic identification was not possible.

Birds collected in this study were herbivorous and/or frugivorous. There was no evidence of arthropods or other animal matter in their diet. Only 5 of 19 birds examined had small quantities of plant material in the esophagus or proventriculus. All had considerable quantities of leaves and/or fruits in the gizzard. Twenty-five species of plants were recovered (Table 1). The predominant food item, based on frequency of recovery from individual birds, was the leaves of several plant species, especially daisies (Aphanostephus sp.) and throughworth (Eupatorium sp.) (42% of individuals examined). Often Plain Chachalaca gizzards were considerably distended with leaves tightly packed in a layered fashion. Macerated and partially digested leaves were found in the remainder of the lower digestive tract. The fruit of the hackberry (Celtis laevigata) occurred frequently (26%). Because the contents of the gizzard often consisted of the mixed, partially digested, or macerated remains of several plant species which could only be identified microscopically, it was not possible to quantify volumetrically the food items observed in most birds. Traces of at least 9 additional plant species were recovered, but these could not be identified because of inadequate taxonomic characteristics.

Marion (1976) concluded that the Plain Chachalaca feeds on a wide range of succulent plant materials and very little animal matter. This is substantiated by our study and suggests that this bird may indiscriminately feed on an even wider range of plants. Only 2 of 42 identified plant species were common to both studies.—ZAN D. CHRISTEN-
### Table 1

**Eosophageal and Gizzard Contents of 19 Plain Chachalacas from the Lower Rio Grande Valley, Texas**

<table>
<thead>
<tr>
<th>Food Item</th>
<th>No. of individuals in which taxa were found</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Leguminosae</strong></td>
<td></td>
</tr>
<tr>
<td>Locoweed (<em>Astragalus sp.</em>)</td>
<td>1</td>
</tr>
<tr>
<td>Honey Mesquite (<em>Prosopis glandulosa</em>)</td>
<td>1</td>
</tr>
<tr>
<td>Black Brush (<em>Acacia rigidula</em>)</td>
<td>3</td>
</tr>
<tr>
<td><strong>Asclepiadaceae</strong></td>
<td></td>
</tr>
<tr>
<td>Milkweed (<em>Asclepias sp.</em>)</td>
<td>1</td>
</tr>
<tr>
<td><strong>Rhamnaceae</strong></td>
<td></td>
</tr>
<tr>
<td>Brasil (<em>Condalia hookeri</em>)</td>
<td>3</td>
</tr>
<tr>
<td><strong>Solanaceae</strong></td>
<td></td>
</tr>
<tr>
<td>Ground Cherry (<em>Physalis sp.</em>)</td>
<td>2</td>
</tr>
<tr>
<td><strong>Urticaceae</strong></td>
<td></td>
</tr>
<tr>
<td>Hammerworth (<em>Parietaria pensylvanica</em>)</td>
<td>1</td>
</tr>
<tr>
<td><strong>Onagraceae</strong></td>
<td></td>
</tr>
<tr>
<td>Evening Primrose (<em>Gaura villosa</em>)</td>
<td>1</td>
</tr>
<tr>
<td><strong>Oxalidaceae</strong></td>
<td></td>
</tr>
<tr>
<td>Wood-sorrel (<em>Oxalis dillenii</em>)</td>
<td>1</td>
</tr>
<tr>
<td><strong>Euphorbiaceae</strong></td>
<td></td>
</tr>
<tr>
<td>Croton (<em>Croton sp.</em>)</td>
<td>2</td>
</tr>
<tr>
<td><strong>Compositae</strong></td>
<td></td>
</tr>
<tr>
<td>Lazy Daisy (<em>Aphanostephus sp.</em>)</td>
<td>8</td>
</tr>
<tr>
<td>Throughworth (<em>Eupatorium sp.</em>)</td>
<td>8</td>
</tr>
<tr>
<td>Mexican Hat (<em>Ratibida peduncularis</em>)</td>
<td>1</td>
</tr>
<tr>
<td>Abrojo (<em>Xanthium strumarium</em>)</td>
<td>1</td>
</tr>
<tr>
<td>Zexmenia (<em>Zexmenia hispida</em>)</td>
<td>1</td>
</tr>
<tr>
<td><strong>Ulmaceae</strong></td>
<td></td>
</tr>
<tr>
<td>Hackberry (<em>Celtis laevigata</em>)</td>
<td>5</td>
</tr>
<tr>
<td><strong>Unidentified Plant Material</strong></td>
<td>9</td>
</tr>
</tbody>
</table>

* Leaves
** Fruit
↑ Includes 9 species of plants.

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Herring Gulls stealing prey from Parasitic Jaegers.—Piracy is well-known among seabirds and is particularly common in the jaegers (Stercorariidae) and gulls (Laridae) (e.g., Bent, U.S. Natl. Mus. Bull. 113, 1921; Belopol’skii, Ecology of Sea Colony Birds of the Barents Sea, translated from Russian, Israel Program for Scientific Translations, Jerusalem, 1961; Hatch, Auk 87:244–254, 1970). Whereas instances of jaegers stealing food from gulls are well documented, reports of gulls stealing food from jaegers by direct attack are sparse. Parmelee and MacDonald (Natl. Mus. Canada Bull. 169:61, 1960) reported Glaucous Gulls (Larus hyperboreus) in the High Arctic attacking and stealing food from Long-tailed Jaegers (Stercorarius longicaudus) which had been foraging at the garbage dump at Eureka, Ellesmere Island. Belopol’skii (op. cit., p. 271) cited cases where Mew Gulls (L. canus) snatched fish dropped by birds being pursued by a jaeger.

This note describes observations of Herring Gulls (L. argentatus) stealing shorebird prey from Parasitic Jaegers (S. parasiticus), at North Point, Ontario, (51°29'N 80°27'W), on the southwest coast of James Bay, 27 km NE of Moosonee, during July and August in 1975 and 1976. Parasitic Jaegers are regular though not numerous migrants on this part of the coast (Manning, Natl. Mus. Canada Bull. 125:57, 1952; pers. obs.), and they prey regularly on small sandpipers which migrate through the area. On 5 August 1975, I was near the edge of the saltmarsh on the upper tidal flats at North Point when the approach of 2 light-phase Parasitic Jaegers was heralded by widespread panic flights amongst small parties of Semipalmated Sandpipers (Calidris pusilla), White-rumped Sandpipers (C. fuscicollis), Dunlin (C. alpina), and Red Knots (C. canutus). Each jaeger started chasing a Semipalmated Sandpiper, but 1 jaeger soon broke off to join the other and after a brief and dashing chase, in which the peep nearly escaped several times, 1 jaeger struck the Semipalmated Sandpiper, knocking it to the ground. The 2 jaegers landed near their prey and were about to eat it, when an adult Herring Gull swooped down, seized the sandpiper and flew off. The jaegers made no attempt to defend their prey, but simply continued their flight up the coast.

On 10 August 1976, I observed 2 Parasitic Jaegers hunting shorebirds along the edge of the saltmarsh and over a stony section of tidal flats. The jaegers pursued first a Semipalmated Sandpiper and then a Dunlin, both of which escaped, even though the flying ability of the latter appeared impaired owing to its being in heavy primary molt. The 2 jaegers then singled out another Semipalmated Sandpiper and, after a brief chase, succeeded in knocking it from the air. As the jaegers landed near the peep, an adult Herring Gull appeared, swooped down, carried off the prey and ate it after landing several hundred meters away. The jaegers gave up their prey immediately to the gull without any apparent resistance. They resumed their hunt, abandoning 1 Semipalmated Sandpiper which flew very close to me during the chase, before moving away along the tide edge. About 40 min later, 2 jaegers reappeared, hunting as a pair. They singled out another Semipalmated Sandpiper and the chase ended as 1 jaeger swooped upwards, seized the peep in mid-air and swallowed it without landing. The jaegers squabbled briefly and then started another chase. An adult Herring Gull flew rapidly towards the jaegers from the tide edge several hundred meters away and followed the hunt closely. The jaegers gave up the chase and flew off down the coast, being followed by the gull.

On 11 August 1976, I observed a Parasitic Jaeger chasing a flock of approximately 1,500 Semipalmated Sandpipers on the edge of the saltmarsh at high tide. The jaeger captured a peep by striking it from the air into the water near the shore, landed, and
presumably swallowed the prey. An adult Herring Gull flew rapidly towards the jaeger, which took off quickly, but the gull soon caught up with it. The jaeger managed to stay above the gull and outmaneuvered it successfully. The technique of gaining height and staying above a predator to avoid capture has been noted by Rudebeck (Oikos 2: 65-88; 3:204-231, 1950-51) and Campbell (Condor 77:485, 1975). The gull broke off its chase and landed on the water.

Incidents where gulls actively pursue jaegers and steal their food are apparently not widespread, and the submissive behavior of the jaegers in giving up their prey at North Point is of interest in this context. Parasitic Jaegers breed on arctic tundra, where small birds, including passerines and shorebirds, comprise the major portion of their diet (Maher, Pac. Coast Avif. No. 37, 1974). For most of the remainder of the year the species is pelagic and obtains much food through piracy. While on the tundra, the jaeger is unlikely to come into contact with any concentrations of gulls, whereas at sea, the jaeger assumes the role of the aggressor in stealing food from gulls. On the flats on James Bay, however, jaegers can find an abundant food supply (small sandpipers) which they are accustomed to and adept at catching, but do so in areas where they may come into contact with local concentrations of gulls. Hatch (Auk 87:244-254, 1970) noted that gulls stealing fish from terns appeared to be more responsive to another gull chasing a tern than to a tern with a fish, suggesting that the sight of a chase may stimulate a gull to investigate a possible food source. A similar behavioral response of Herring Gulls to jaegers chasing shorebird prey on the coastal flats in James Bay could have led to the observed instances of piracy. I do not know whether piracy is general amongst adult Herring Gulls on James Bay, or whether the instances observed involved 1 or a few individuals which had specialized in this behavior, as may occur elsewhere (Hatch, op. cit.).

The lack of response by jaegers to piracy by gulls may also have reflected an extremely abundant and easily obtainable food resource, so that it was not worthwhile for jaegers to expend energy and perhaps risk injury in fleeing or defending their prey. On the other hand, the food item was large enough to make it energetically worthwhile for the gull to respond to hunting jaegers and to attempt to steal their prey. These considerations were thought to be of importance in the examples of piracy discussed by Bird et al. (Wilson Bull. 85:480-482, 1973) and by Payne and Howe (Wilson Bull. 88:349-351, 1976).

It thus appears that cleptoparasitism involving unusual pairs of species may appear where they are brought together in the presence of locally abundant prey large enough to be worthwhile stealing by the aggressor and plentiful enough not to be worthwhile defending by the victim.

I should like to thank H. Boyd for critical comments on an earlier version of the manuscript.—R. I. G. Morrison, Canadian Wildlife Service, 2721 Highway 31, Ottawa, Ontario, Canada, K1G 3Z7. Accepted 30 Sept. 1977.


The use of feeding areas outside of the territory of breeding Black Oystercatchers.—Cleland Island, off the west coast of Vancouver Island, B.C. is a breeding site for approximately 50 pairs of Black Oystercatchers (Haematopus bachmani). For 3 consecutive summers (1970-73) I investigated the foraging of these birds and I observed that, at times, 1 or both of a pair of breeding birds leave their territory and fly to a
distant reef or island. At first I thought that this only occurred early in the season when pairs were still establishing territories and winter flight patterns were still operating. In this note I report observations of extra-territorial feeding during all stages of the breeding season. The use of distant feeding areas by oystercatchers was noted by Webster (Wilson Bull. 53:141–156, 1941) during the incubation period. His observations off the Alaskan coast suggested that such trips were discontinued as soon as the chicks were hatched.

I observed 24 trips involving 6 different pairs of breeding birds. Trips on 26 May and 2 June were made by both members of a pair whose territory was then unoccupied. Twenty-two trips occurred later in the season and involved only 1 of each pair. Three of these trips were made when eggs were in the nest while the other 19 trips were made when chicks were present.

In each case, 1 of the pair would be foraging or roosting and then would give a "queep, queep" call and take off on a consistent route to a distant reef. It seemed that different birds headed for different reefs. In one observation period, a member of one pair left in a straight line course toward an island approximately 1 km to the northeast while a bird from another pair left its territory heading north toward another island. The birds could be observed through a telescope and they often followed predictable routes until out of sight. The birds often spent 20 min or more away from the nest and they often returned carrying a large food item for the young. This was usually a mussel (Mytilus californianus) but sometimes was a large limpet (Notoacmea sp.). In a few cases the birds returned without food. Such trips were observed in both morning and afternoon, and in all months, May to August inclusive.

Since the Black Oystercatcher spends considerable time defending a large territory which usually includes a section of shore for feeding, it seems unusual for the birds to leave and search for food elsewhere. On the other hand, Heppleston (J. Anim. Ecol. 40:651–672, 1971) found evidence that European Oystercatchers (H. ostralegus) were at times unable to obtain sufficient food from shore habitats and had to supplement their diet with food from elsewhere; in this case, neighboring fields. My observations suggest that trips made by birds on Cleland Island may be linked to the availability of food in the feeding territory. The birds fed mainly on intertidal molluscs, especially on mussels (M. californianus and M. edulis) throughout the year (Hartwick, Can. J. Zool. 54:142–155, 1976). Their foraging activity generally shows a bimodal pattern with a peak before and after low tide. Such a pattern has been observed in a number of species of oystercatchers. New Zealand oystercatchers (H. unicolor and H. ostralegus finschi) show a similar pattern over the tidal cycle when feeding on tua-tuas (Amphidesma subtriangulatum) (Baker, J. Life Sci. Contr. R. Ont. Mus. No. 96, 1974). Such patterns have also been noted by Tinbergen and Norton-Griffiths (Br. Birds 57: 64–70, 1964) for European Oystercatchers feeding on mussels. Based on feeding rate data, Norton-Griffiths (Behaviour 34:55–114, 1969) found no connection between the pause in feeding activities and the availability of food. In the case of Black Oystercatchers, slack water at low tide is usually accompanied by diminished feeding rates or often by roosting. Low tide seems to be a period of low food availability. In the case of a low, low tide, especially in the summer, most of the intertidal area is in the process of drying and no mussels are available except in pools. Mussels begin gaping as the tide rises and they become washed by waves at which time they are again vulnerable to the Black Oystercatcher (Hartwick, Can. J. Zool. 54:142–155, 1976). Although the birds feed on many other items, their foraging appears to be keyed to the vulnerability of their major prey, the mussel. Thirteen of the 22 trips were made within
an hour of low tide and those trips that were made at other times occurred either before
the mussel bed was washed by waves or during tides of short range and high surf when
there was little opportunity for the birds to forage safely.

No attempts were made to follow the birds and I can only assume that foraging
was better in the areas they headed for. Certainly large mussels were not available in
their feeding territories when they were observed to bring such items back on these
trips. While the energetic advantages of such trips seem questionable, such trips ap-
ppear to be a normal part of the activities of breeding oystercatchers. The significance
and relationship of these trips to the general dispersion patterns of the species must
remain in question.—E. B. HARTWICK, Dept. of Biological Sciences, Simon Fraser Univ.,
Burnaby, B.C. V5A 1S6.


Screech Owl predation on a Common Flicker nest.—Two cypress Wood Duck
(Aix sponsa) nesting boxes (3 m above ground level and facing opposite directions)
erected on the same creosote pole at Pearl River Waterfowl Refuge in Mississippi, were
selected by a red phase Screech Owl (Otus asio) and a Common Flicker (Colaptes
auratus) as nest sites in April 1977. The owl laid 2 eggs and was incubating them in
1 nest box when the flicker began laying a series of 6 eggs in the other box. The owlets
hatched just before the flicker young did. The owl fed the owlets other food items
until she discovered the flickers in the next box. Five babies had hatched and begged
constantly. The owl flew into the flickers’ nest box and removed the young birds 1 by 1
to feed her owlets. This process took several days. The flickers continued during this
time to feed their surviving young. Not until all flicker young were taken by the owl
did they fail to return to the nest box. Half-eaten flickers were found in the owl nest box.
—MARY C. LANDIN, USAE Waterways Experiment Station, Vicksburg, MS 39180. Ac-


Red Bobwhites in Oklahoma.—On 2 September 1973, I collected an erythristic
female Bobwhite (Colinus virginianus) 3 km NE of Southard (Blaine Co.), west-central
Oklahoma. Its plumage was deep chestnut-red except for 3 white feathers on the
central upper chest (= “crop patch”) and black markings as follows: median crown
feathers almost totally black, nape feathers moderately so; upper wing coverts, chest
and belly feathers mottled; flank feathers heavily barred; tertials and upper rump
feathers with wide, irregular subterminal bands; upper tail coverts with black narrowly
bordering rachis on either side; under tail coverts heavily mottled, especially toward
the center; legs and bill black. Rectrices, primaries, and secondaries were solid brownish-gray.

Little subcutaneous fat was found during skinning, yet the bird weighed 183.5 g.
Average weight of 8 adult females in the University of Oklahoma collection was 174.2 g.
so the specimen appeared to be healthy. The single intrauterine egg measured 26 × 20
mm (fully developed eggs \( n = 59 \)) in the U.S. National Museum averaged 30 × 24 mm
(Bent, U.S. Natl. Mus. Bull. 162, 1932)). Measurements were: wing 114, tail 61, culmen
15, and tarsus 30 mm. The specimen is in the Cameron University collection (CUMZ 465).

The red quail was in a covey with 6 or 7 normally-colored Bobwhites in a sumac (Rhus sp.) thicket along a railroad right-of-way. Permian Red-bed soils here were deeply eroded, exposing numerous gypsum outcappings, and covered by overgrazed midgrassies (primarily Little Bluestem, Andropogon scoparius), scattered mesquite (Prosopis juliflora), and redcedar (Juniperus virginiana). Plum (Prunus sp.) and sumac were common in low areas.

George Wint, long-time director of the state game farm, was unaware of any released red quail in Oklahoma during the past (pers. comm.), and the landowner likewise knew of no such releases on or near his property.

During the third week of November 1973 a covey of 6 Bobwhites containing 2 red birds appeared in the W. B. Wise yard in Norman (Cleveland Co.). They remained in the area throughout winter and were last seen about 15 April 1974. Color photos on file in the Cameron Museum clearly show their chestnut color, white crop patches, and black legs and bills.

Crosses with captive red Bobwhites near Thomasville, Georgia from 1934–1936 indicated that the red color is incompletely dominant and not sex-linked (Cole et al., Auk 66:28–35, 1949).

Buckle (Am. Field 107:444, 1927) described a pair of red quail collected near Grand Junction, Tennessee from a covey of 15 or 20 containing 7 red birds (Stoddard, The Bobwhite Quail, Chas. Scribner’s Sons, N.Y., 1931:86), and Aldrich (Auk 65:493–508, 1946) summarized early red Bobwhite records in the U.S. In all cases, however, specimens were either of the northeastern race (C. v. marilandicus) or the eastern race (C. v. mexicanus); measurements and geographic location suggest that the Oklahoma birds are assignable to C. v. taylori, the Great Plains race from which erythris has apparently not been reported (Aldrich, op. cit.).—Jack D. Tyler, Dept. of Biology, Cameron Univ., Lawton, OK 73501. Accepted 3 Aug. 1976.


Asynchrony of hatching in Red-winged Blackbirds and survival of late and early hatching birds.—Lack (Ibis 89:302–352, 1947) argued that the asynchrony of hatching observed in various birds of prey could reduce the loss of nestlings during a food shortage. The last born young are put at a competitive disadvantage that insures their demise and leaves the remaining young with sufficient food for development. That these birds of prey begin incubation before the clutch is complete and that the last born young do starve except when food is plentiful support this hypothesis. Lack suggested that such a brood reduction after hatching would be primarily of value to species with long fledging periods that are not subject to high rates of nest predation. Runtling and brood reduction have however been observed in numerous, small passerines including the Red-winged Blackbird (Agelaius phoenicus) (Holcomb and Twiest, Bird-Banding 42:1–17, 1971), and so too incubation before the completion of the clutch (Holcomb, Wilson Bull. 87:450–460, 1974). Data I collected during the spring of 1976 from a population of marsh nesting Red-winged Blackbirds in the LaRue Swamp, Union County, Illinois further document the relationship between hatching rank and nestling survival.
Table 1

Nestling Mortality of First-, Second-, and Third-day Hatchlings in 41 Successful Red-winged Blackbird Nests

<table>
<thead>
<tr>
<th>Nestlings</th>
<th>Total</th>
<th>Starved</th>
<th>Vanished</th>
<th>Combined lost</th>
</tr>
</thead>
<tbody>
<tr>
<td>First-day</td>
<td>77</td>
<td>0</td>
<td>2 (2.6%)</td>
<td>2 (2.6%)</td>
</tr>
<tr>
<td>Second-day</td>
<td>53</td>
<td>11 (20.8%)</td>
<td>5 (9.4%)</td>
<td>16 (30.2%)</td>
</tr>
<tr>
<td>Third-day</td>
<td>8</td>
<td>3 (37.5%)</td>
<td>1 (12.5%)</td>
<td>4 (50.0%)</td>
</tr>
<tr>
<td>Second- &amp; third-day</td>
<td>61</td>
<td>14 (23.0%)</td>
<td>6 (9.8%)</td>
<td>20 (32.8%)</td>
</tr>
<tr>
<td>All</td>
<td>138</td>
<td>14 (10.1%)</td>
<td>8 (5.8%)</td>
<td>22 (15.9%)</td>
</tr>
</tbody>
</table>

Nests which I discovered before any of the eggs had hatched were visited daily. Hatchlings were marked for individual identification, and the nestlings were examined and weighed daily. If some but not all of the eggs hatched between daily visits, those that hatched in the first 24 h period were categorized as “first-day hatchlings,” those that hatched in the next 24 h were categorized as “second-day hatchlings” and any that hatched in the third 24 h were categorized as “third-day hatchlings.” Nestlings which failed to fledge were placed into 2 categories: “starved” and “vanished.” Starved individuals disappeared or were found dead in the nest after failing to gain 4 g in 2 days. They typically exhibited a continuous begging behavior when handled and were 2 or more g lighter than other chicks in the same nest. Nestlings that disappeared while maintaining a normal growth of 3 to 4 g per day were listed as vanished. Six of 8 vanished birds were smaller than their siblings.

Of nests examined daily for hatching, 65 were successful. In 41 of these, there were second-day hatchlings. In 8 there were also third-day hatchlings. The fate of the

Table 2

Comparison of Growth of First- with Second- and Third-day Hatching Nestlings

<table>
<thead>
<tr>
<th>Day</th>
<th>First-day hatchlings</th>
<th>Second- and third-day hatchlings</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean weight (g)</td>
<td>Mean weight (g)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>3.47</td>
<td>3.58</td>
<td>.5354</td>
</tr>
<tr>
<td>1</td>
<td>5.65</td>
<td>4.77</td>
<td>.0001*</td>
</tr>
<tr>
<td>2</td>
<td>9.05</td>
<td>7.29</td>
<td>.0001*</td>
</tr>
<tr>
<td>3</td>
<td>12.93</td>
<td>10.57</td>
<td>.0001*</td>
</tr>
<tr>
<td>4</td>
<td>17.02</td>
<td>14.32</td>
<td>.0001*</td>
</tr>
<tr>
<td>5</td>
<td>21.04</td>
<td>18.13</td>
<td>.0003*</td>
</tr>
<tr>
<td>6</td>
<td>25.89</td>
<td>21.89</td>
<td>.0001*</td>
</tr>
<tr>
<td>7</td>
<td>28.67</td>
<td>25.39</td>
<td>.008*</td>
</tr>
<tr>
<td>8</td>
<td>30.70</td>
<td>27.09</td>
<td>.008*</td>
</tr>
<tr>
<td>9</td>
<td>31.94</td>
<td>29.86</td>
<td>.2713</td>
</tr>
</tbody>
</table>

* Indicates significance at the p = 0.05 level as determined by the Mann-Whitney U-Test.
nestlings from these 41 nests, according to whether they were first-, second-, or third-day hatchlings is illustrated in Table 1. Of 77 first-day hatchlings, 2 vanished, a total loss of 2.6%. Of 61 second- and third-day hatchlings, 14 starved and 6 vanished for a total loss of 32.8%. This loss of nestlings occurred throughout the brooding period. A nestling with a few hours head start enjoys a size advantage over later hatching birds. Four birds that were discovered hatching and re-examined 5 h after hatching had gained 1.5 g from a hatching weight of 3.0 g. The mean weights of second- and third-day hatching nestlings were smaller than those of first-day hatching nestlings throughout the nestling period (Table 2), though by day 9 the weights of surviving first-, second-, and third-day nestlings were not significantly different.—Charles Streihl, Dept. of Zoology, Univ. of North Carolina, Chapel Hill 27514. Accepted 8 Aug. 1977.


Weather-related mortality of blackbirds and Starlings in a Kentucky roosting congregation.—Associated with an over-night storm in Illinois, Odum and Pitelka (Auk 56:451–455, 1939) found approximately 4.0% mortality among blackbirds and Starlings (Sturnus vulgaris) in a roosting congregation containing 25,000 birds. The rate of mortality was much higher among Common Grackles (Quiscalus quiscula) and Brown-headed Cowbirds (Molothrus ater) than among Starlings. Also, MacReynolds (Auk 34:338–340, 1917) found 30 dead Common Grackles at a roosting site in Pennsylvania after a heavy snow storm, and Forbush (Birds of Massachusetts and other New England States, Part 2, Mass. Dept. Agr., Boston, Mass. 1927:409) found about 500 dead Starlings at a roosting site in Massachusetts after a winter storm. On the morning of 12 January 1977, I visited the roosting site near Russellville, Kentucky, of a congregation of blackbirds and Starlings and found 38 dead birds on top of the snow. In walking over the same route the following day, 26 more dead birds were found.

The dead birds were found in walking about 380 m through the roosting site each day, with the size of the sample limited by the difficulty in walking through the vines and underbrush. I was 2–5 m from the 64 birds when first spotting them, with an average of 3.6 m. Thus, I covered a strip about 7.2 m wide and in walking 380 m covered an area of about 0.3 ha. The roosting congregation covered about 1.6 ha, and a total of about 374 birds thus probably died on the 2 nights. The total congregation contained an estimated 45,000 birds, and the mortality rate for the 2 nights was approximately 0.8%.

The congregation contained about 0.8% Starlings, but 84.4% of the birds found dead were Starlings, with the rate of mortality 106 times the proportion in the congregation. About 0.9% of the congregation was Red-winged Blackbirds (Agelaius phoeniceus), with 6.3% of the birds found dead being of this species and the rate of mortality 7 times the proportion represented in the congregation. About 98% of the birds in the roosting congregation were Common Grackles, but only 9.4% of the dead birds were grackles. Thus, unlike the situation reported by Odum and Pitelka (op. cit.) where the rate of mortality was much higher among Common Grackles than Starlings, the rate of mortality I observed was about 9 times higher among Starlings than Common Grackles. Approximately 14,500 Common Grackles left the roosting site on a line headed southward in the evening of 8 January, suggesting that many of the birds responded to environmental stress by southward movement (Stewart, Bird-Banding, in press). The congregation contained about 0.3% Brown-headed Cowbirds, with none found dead.
A total of 25 cm of snow fell during the period 3–10 January, making finding food difficult for the birds. Furthermore, weights of the Starlings found dead at the roosting site were relatively low, the 54 birds averaging 81.4 g; whereas, 22 Starlings shot at mid-day averaged 94.6 g. All of the 6 grackles and 17 of the 54 Starlings found dead at the roosting site contained food in their gizzards, indicating that at least some of them had not died from starvation. More birds were found dead on the morning of 12 January (38) when the lowest temperature during the night had been –24.4°C than in the morning of 13 January (26) when the lowest temperature was –17.2°C. I think that the mortality can be considered to have been weather-related. But, when there had been no shooting following 2 heavy snowfalls in North Carolina, I searched at blackbird-Starling roosting sites without finding any dead birds.

Many Starlings came to the roosting site each evening only to leave immediately to go to spend the night in a nearby barn. Nine dead Starlings were found in the barn on the mornings of 12 and 13 January. Since approximately 2500 Starlings roosted in the barn, the rate of mortality (0.4%) was much lower among Starlings in the barn than among those roosting in the trees (15%). The owner of the barn reported that the Starlings roosted in the barn only in unusually cold weather. — Paul A. Stewart, 203 Moorland Drive, Oxford, North Carolina 27565. Accepted 5 Aug. 1977.


An observation of polygyny in the Common Yellowthroat. — During the summer of 1967 at the American Museum of Natural History’s Kalbfleisch Field Research Station at Huntingdon, New York, we observed a color-banded male Common Yellowthroat (Geothlypis trichas) mated with 2 color-banded females, each of which successfully fledged young (on 5 and 10 July). On 2 June, the male and female A were observed feeding in a hedgerow that divided 2 fallow fields. On 14 June, the male was observed aiding a second female (B) in the early stages of building a nest in the field to the south of the hedgerow. On 18 June, the male was again observed feeding with female A who had a clutch of 4 eggs in the field to the north of the hedgerow. Observations made on 26 June revealed that the male was feeding the recently hatched nestlings of A and making infrequent visits to the vicinity of B who was observed incubating a clutch of 4 eggs.

Extensive observations on 4 and 5 July revealed that the male continued to assist female A in feeding her young, but spent approximately 25% of his time singing in the hedgerow and visiting female B, presumably to assist feeding her nestlings. On 8 July, the male divided his time equally between both fields. During the entire day of 14 July, the male fed young with female B except for 2 short visits to female A.

Female A and her young were last observed on 19 July. The male remained with female B in the south field and intermittently fed the young during the remainder of July and August. The male gave the flight song on several occasions, but no further nesting attempts were discovered in the area.

The territory of this male yellowthroat was about 1.2 ha, approximately twice the size of that reported for monogamous males (Stewart, 1953, Wilson Bull, 65:99–115). Breeding bird censuses of the south field during the 2 previous summers (unpubl. reports Kalbfleisch Field Research Station Am. Mus. Nat. Hist.) reported 2 male yellowthroats occupying territories comparable to those reported by Stewart. During our study, only the one male was present and the remainder of the south field was unoccupied by
yellowthroats (The north field had not been censused previously). This suggests that reduced intra-specific competition, due to a shortage of males, may have permitted the maintenance of a larger territory and second female. Nolan (1963, Proc. XIII Int. Ornithol. Congr., 329–337) cites a similar case with a male Prairie Warbler (Dendroica discolor) that was forced to give up half of a large territory and a second nesting female to a male that appeared 3 weeks into the breeding season.

These observations were made while we were participants in NSF URP grant GY-989. We are indebted to Edward Gilman for assistance with observations.—George V. N. Powell, Dept. of Zoology, Univ. of California, Davis 95616, and H. Lee Jones, Dept. of Zoology, Univ. of California, Los Angeles 90024. Accepted 15 Aug. 1977.

DOUBLE-BROODEDNESS IN PURPLE MARTINS: ADDENDUM

In Charles R. Brown's paper on double-broodedness in Purple Martins, Wilson Bull. 90: 239–247, 1978, the following paragraph was inadvertently omitted from the "Observations" section:

1977: Two color-handed pairs of Purple Martins successfully fledged second broods of 4 and 5 young on 27 and 29 July, respectively. These pairs previously had fledged first broods of 5 young each. These pairs wore bands which had been painted distinctive colors. The identity of these individuals was confirmed by observation and (for some) capture during both broods. Time did not permit a detailed analysis of martin populations and environmental conditions at the colony in 1977, since most field work was performed at another Purple Martin colony that year. But behavior of the second broods in 1977 closely paralleled behavior of the 1976 broods. (Additional second broods were noted at another Sherman colony in 1977.)
ORNITHOLOGICAL LITERATURE

AVIAN BREEDING CYCLES. By R. K. Murton and N. J. Westwood. Oxford University Press, Oxford, England, 1977: xiii + 594 pp., 25 tables, 191 figures, 26 black and white photographs, 5 appendices, bibliography, species index, author index, subject index. $48.00.—This review text is designed to stimulate research, and although addressed to "post graduate workers and senior undergraduates", the authors also hope that it will appeal to ornithologists in general. In Chapter 1, the authors state their basic objectives: (1) "to illuminate some of the patterns of ecological adaptations that result from restraints imposed by complex physiological mechanisms", (2) "to persuade physiologists to relate their experiments to the natural conditions under which their subjects live", and (3) to provide a starting point and stimulus for a multi-disciplinary approach in avian breeding biology and eco-physiology. My overall impression is that they are more than moderately successful on the first point but only time will tell on the last 2.

The 16 chapters may be roughly divided into 5 divisions each dealing with a specific aspect of avian breeding cycles. Chapter 1 serves as an introduction and sets the stage for the rest of the book. Here the distinction is made between ultimate and proximate factors in avian breeding cycles. Ultimate factors "have survival value and not much causal function", while proximate factors "provide the actual mechanism whereby breeding adaptations are achieved." A short section on survival rates leads to Ricklefs' notion (Nature, 223:922–925, 1969) that natural selection will attempt to minimize total mortality. A summary figure (Fig. 1.8) illustrates how environmental stimuli and internal stimuli are integrated to regulate reproduction. Most of the rest of the book looks at the various aspects of this figure.

The next section, Chapters 2–6, reviews basic anatomy and the endocrine basis of reproduction. The authors state that the highly technical terminology of this section is "liable to deter all except specialist readers." This is true! It is here that the general ornithologist may become, if not totally lost, at least bored and befuddled. In my opinion, Chapters 2–4 and 5–6 could be greatly shortened and combined. The latter 2 chapters do, however, provide some good information on the role of the endocrine glands in such behavior as pair formation, courtship, nest building, and incubation. It is unfortunate that most of this work has only been done on pigeons, chickens, and canaries.

Chapters 7 and 8 deal with energy budgets, and it is here that the book really gets going. The authors examine a wide range of strategies developed by birds to maximize their efficiency in coping with the series of peaks in energy demand that occur during a year. Such peaks include migration, molting, reproduction, and thermoregulation during periods of temperature stress. The metabolic rates section includes a summary of Ken-deigh's study (Wilson Bull., 81:441–449, 1969) on Passer domesticus. An interesting section on energy partitioning is drawn from numerous studies and looks at evolutionary trends (e.g., British thrushes). The discussion on migration and fat stores is incomplete and lacking in several aspects. How one can talk about fat deposition, migration and Zugunruhe without mentioning King and Farner's classic review (Ann. New York Acad. Sci., 131:422–440, 1968) or about Redpolls (Carduelis flammea) without mention of George West's work is beyond me. The section on clutch size is fairly complete and follows the Lack hypothesis. The authors dismiss Wynne-Edwards' ideas in 3 sentences on page 199. I feel that a more complete treatment of this debate is warranted and for this reason I was somewhat disappointed with this part of the book. Later, in Chapter 16, the Wynne-Edwards theory is presented in more detail, but his ideas on
clutch size are basically ignored. In their discussion of nestling growth, the authors summarize some of Ricklefs’ work stating that the full food gathering potential of the adults cannot be achieved during the early stages of the season, perhaps because the parents must initially find time to brood. An equally likely assumption, apparently overlooked by the authors, is that food could be less available during spring and early summer, thus reducing the foraging efficiency of adult birds. A discussion of frugivory in the section on incubation time and nestling growth would have added a great deal.

The next major division of the book contains 6 chapters dealing with breeding cycles and photoperiodism. The last chapter of this division, on the evolutionary aspects of photoperiodism, is the highlight of this part of the book. Here the authors draw on the vast amount of controlled research done on waterfowl at the Wildfowl Trust at Slimbridge, England. The section on desert breeding is of interest, but in no way compares to Serventy’s review in Avian Biology Vol. I.

The last 2 chapters of the book, Sexual Selection and the Pair Bond, and Population Regulation, are its best. These are the only chapters that keep my interest throughout. The sexual selection chapter builds on Fisher’s theory (The Genetical Theory of Natural Selection, Clarendon Press, Oxford, 1930), adding the work of O’Donald, Trivers and others. The authors reject Zahavi’s notion (Proc. 16th Int. Orn. Congr. 685-693, 1976) of the handicap principle. However, a better discussion of this is found in The Selfish Gene by R. Dawkins. The section on sexual dimorphism is nearly 10 pages long, yet surprisingly incomplete. Murton and Westwood present Selandar’s review paper (Condor 68:113-151, 1966) and Reynolds’ work on Accipiter Hawks (Condor 74:191-197, 1972), but overlook the rather interesting work by Mosher and Matray (Auk 96:325-341, 1974) on Broad-winged Hawks, and Snyder and Wiley’s important review of Sexual Dimorphism in Hawks and Owls of North America (Ornith. Monogr. no. 20, 1976). I found the section on polymorphisms to be highly illuminating, especially the review of Cooch and Cooke’s numerous papers on geese. In their discussion of polyandry and sex reversal, the authors state that this mating system is rare, having evolved only 6 times, but their list does not include the Phalaropes which they state on page 440 are polyandrous. The short section on cooperative breeding contains a paragraph or two on ritualized fighting that is far too brief to be of much value. Again readers are directed to Dawkin’s book for a more thorough discussion. I was surprised that the section on brood parasitism did not include any of Steven Rothstein’s work. The population regulation chapter summarizes much of Murton’s work with Wood Pigeons, Southern’s work with the Tawny Owl, and Watson, Miller and others on the Red Grouse. While nothing new is presented here, it is an excellent review.

My overall impression of the book is that it has its highs and lows. Certainly the last 2 chapters are highs but the first six are lows. The writing style makes the book tedious to read, but rather complete subject, species, and author indices make it a valuable reference book. A count of the entries in the bibliography gave a total of approximately 1631! A random check of 363 references revealed 11 errors or 3.03%, which projects to a total of 49 for the entire bibliography. This is a surprisingly high number of errors, especially since the authors stated that they owed Mrs. M. Haas a special debt of gratitude for compiling and checking the bibliography! These errors could be removed in a second printing. Typographic errors are minimal and most of the scientific names are correctly spelled. The book is slanted towards Old World birds, with primary emphasis on Palearctic and Ethiopian faunas. A random check of the species index (n = 200) found 157 or 79% of the birds listed to be Old World forms. For North American ornithologists, this provides a refreshing opportunity to
learn about unfamiliar birds, but the authors have missed a great deal of work that is pertinent to their topic on New World birds, and in this regard the book is definitely lacking.

In light of the very high price of this book, I wish to make a few comments. The book is poorly bound (mine started to crack while I was reviewing it), printed on poor quality paper, the right margins are not justified, and there are no color plates. Perhaps only one or two of the black and white photographs are really necessary. (The picture of House Sparrows showing feather wear, Fig. 15.4, is the only one that I feel warrants the cost of inclusion.) For the cost of this book, I can pay my yearly dues for W.O.S., C.O.S., and A.O.U! With this in mind, I would not have a copy of my own had it not been sent to me to review. I certainly could not afford to buy it even with my high salary as an Assistant Professor, and I don't see how students could either.

In summary, even with its faults, this is an excellent but grossly overpriced review of avian breeding cycles. Although the book probably will never be used as a classroom text, the more conscientious teachers will undoubtedly use it as a reference for preparing lectures. Some of the material is covered more thoroughly elsewhere (e.g. Avian Biology) but still much of the book is quite well done and much needed. However, it is not worth the price.—ROBERT C. WHITMORE.


BIRD FLIGHT. By Georg Rüppell. Van Nostrand Reinhold Co., New York, 1978: 191 pp., 239 illustrations. $18.95.—This is a fine, nontechnical introduction to the flight of birds. Originally published in Germany as Vogelflug, the text has been translated into English by Marguerite A. Biederman-Thorson, who has rendered it effectively into an easy conversational style totally lacking the cumbersome, stilted prose that often results from such efforts. The author begins by introducing the general phenomenon of flight as seen in animals other than birds, and the early attempts in various countries to understand the flight of birds and to apply these principles to the development of aircraft. Then follows a discussion of avian anatomy in relation to flight. This is generally clear and accurate, though in places the desire to keep things simple has led to minor errors, such as calling the tibiotarsus the tibia, or referring to the foramen triróseo as a hole in a bone. The emphasis in this chapter is, naturally, on bones, muscles, and feathers. Next comes a short and painless chapter on aerodynamics, in which the author is refreshingly candid about how this subject reveals the general basis of bird flight but cannot as yet provide a detailed or quantitative understanding of complex aerial maneuvers. Following this, several chapters examine in detail the different modes of bird flight, the special problems of taking off and landing, and the adaptive specializations of birds for different methods of flight used in finding and capturing food, and escaping enemies. Rüppell emphasizes how the evolution of specializations for certain types of flight occur at a price of reduced effectiveness in other modes; the familiar idea of specialists and generalists is explained effectively here. Finally, a brief glossary explains various technical terms used in the text.

The book is unusually well written. The author is skilled at using the effective technique of introducing new ideas by reference to familiar ideas or examples. Still, the heart of the book is the illustrative material, including numerous line drawings in the margins that illustrate matters discussed in the text, especially aerodynamic prin-
principles. The photographs are outstanding, most of them taken by the author at high speed to illustrate specific points made in the text. Rather than being merely decorative, these photographs are closely integrated with the text, and will greatly aid the reader in interpreting the actions of birds seen in the field.

There are a few minor typographical errors. In the references, the paper on Weight, Wing Area, and Skeletal Proportions in Three Accipiters by R. W. Storer is incorrectly attributed to J. H. Storer. In general the recent literature is well reviewed, though I was surprised to see no mention of the studies of D. B. O. Savile. At a time of increasing costs and declining production quality, this book is very well made and well worth the price.—ROBERT J. RAIKOW.


The Hen Harrier. By Donald Watson. T. and A. D. Poyser, Berkhamstead, England, 1977: 299 pp., 4 color plates, numerous drawings, 15 text figs., 4 appendices, 30 tables. About $13.25.—This book is obviously the labor of love of one who has been infatuated with, and spent many hours in the field studying Circus cyaneus. I enjoyed reading the book, probably because of its largely informal, anecdotal style, but as a scientist I often became impatient in seeking real data in the meandering narrative.

The book is organized into 3 parts, of which only the last 2 are numbered. Part 0 includes an introduction and 2 chapters, 1 on the harriers of the world, and 1 on plumages and identification. The first chapter is peculiar in a book on the Hen Harrier and was presumably included so the author could include his observations on the Pied Harrier in Burma, while he served with the military. This chapter has a number of defects, and the serious reader might best skip it and not be put off from reading later chapters which contain carefully gathered, and presented, information. I am not familiar with all the details of the geographic distribution of the various species of harriers but the range maps of C. buffoni and C. cinereous are clearly totally confused with each other. The erroneous maps apparently led the author to state that C. buffoni is the only harrier to breed north and south of the equator (except for C. aeruginosus). C. cinereous also breeds on both sides of the equator. Page 21 is an atrocious black and white plate showing males, females and “immatures” of 10 species of harriers, with each illustration so tiny as to show virtually none of the characteristics of the species. There are separate illustrations of the European and American C. cyaneus, which differ little, and only the European form of C. aeruginosus, from which the Australasian race differs enormously.

The chapter on identification fails to convey, to the non-expert, the difficulty of identifying the European Harriers. In contrast, the 4 pages on albinism and melanism, listing every British specimen, seem excessive. In the absence of known-age birds, I remain unconvinced that male Hen Harriers become lighter in color each year. Individual variation seems as reasonable an explanation.

Part I is entitled “The Hen Harrier” and includes 6 chapters. The history of the species in Britain and Ireland is covered in an almost excessively scholarly, but enjoyable, manner. The bird appears first in a poem by Dunbar in 1504, and the first scientific description appeared in 1544. It was not until 1684 that the male and female were recognized as belonging to the same species, and it was not until 1802 that Montagu described C. pygargus as distinct from C. cyaneus. Maps of the breeding distribution of
the Hen Harrier in the British Isles are presented for a sampling of years between 1875–1975. The species declined dramatically between 1825 and 1865, virtually disappeared by 1900, reappeared in 1946 and showed a steady increase in breeding range through 1975.

Chapter 4 deals with hunting methods, prey selection, and food habits. Many readers will be surprised to find that the diet of Hen Harriers is 96% birds during the breeding season. My only quibble with this chapter is the number of anecdotes indicating that the Hen Harrier will pursue flying birds. In my experience, Harriers, more so than any other hawk, will rarely pursue a flying bird; if prey birds cannot be taken by surprise, they are ignored. Chapters 5 and 6 do a good job on the breeding cycle, from courtship through fledging. The author suggests that pairs with at least one adult that is aggressive to human intruders are more successful in rearing young; he fails to note that this difference is not statistically significant (chi-square, \( p > 0.15 \)). Similarly, he suggests that birds nesting in young conifer plantations are less aggressive than those nesting in moorland, and again my statistical analysis fails to support this (\( p > 0.11 \)). The only mention of statistics in the book is a statement that the sex ratios of nestlings and of fledglings do not differ from unity, yet here the differences come very close to significance (\( p > 0.05 < 0.06 \)). The female-dominated sex ratio may be a factor in producing the occasional to frequent polygyny found in this species; this possibility is not discussed adequately.

Chapter 7, Migration and Winter Distribution, is notable for its analysis of all British banding recoveries. The brief and peculiar Chapter 8 identifies the author as an artist as well as a biologist. I enjoyed it, as I enjoyed and admired most of the black and white vignettes aesthetically scattered through the text. In my opinion, the few color plates are, by comparison, lacking, except those of nestlings which have a certain poignancy.

Part II contains 11 chapters, of which the first 10 deal with the author’s personal experiences with the species in southwest Scotland. This could have been a book in itself. Included in this volume, it is often no more than a repetition and expansion of Part I; I wish that they had been combined. This part does convey, vividly, the excitement of field study, and its trials and tribulations.

A map of the study areas would have helped me keep my mind straight between accounts of area A and area K, etc.; perhaps concern for the safety of the birds kept the author from including even a large-scale map. Chapter 19, on winter roosts, is excellent. The last chapter, appealing for conservation of this controversial species (in Britain), is well done. The very civilized Britons, who criticize the Italians and French for shooting and eating songbirds, might do well to expend their ire on their countrymen who shoot driven Red Grouse, resulting in an industry which persecutes avian predators with a ferocity unequated on this planet—and then they don’t even eat the hawks.

Thirty tables are “conveniently” grouped at the end of the book. I found this luxury quite annoying while reading the book. The bibliography, although not extensive, seems to include most, if not all, the significant references on \( C. cyaneus \), including those published in other languages. Page numbers are not given for citations from journals; this minor and thoughtless omission will be at least an inconvenience to anyone attempting to obtain a reference.

The book is a good review of Hen Harrier biology, contains considerable original information collected by the author and other unpublished data which he managed to obtain from other workers. It is an excellent and thorough work and it belongs on the bookshelf of every raptor enthusiast, professional or amateur. —HELMUT C. MUELLER.
BIRDS OF SOUTHEASTERN MICHIGAN AND SOUTHWESTERN ONTARIO. By Alice H. Kelley, Cranbrook Institute of Science, Bloomfield Hills, Michigan, 1978: 99 pp., 1 map, paper cover. $2.95.—This is a survey of the relative abundance, migration patterns, breeding status, and habitats of 337 species surveyed between 1945 and 1974. The area covered includes Lambton, Kent, and Essex counties in Ontario, and St. Clair, Macomb, Oakland, Wayne, and Monroe counties in Michigan.—R.J.R.

WILDESE Geese. By M. A. Ogilvie. Buteo Books, Vermillion, S.D., 1978: 350 pp. $25.00.—This book is certain to become a significant element of all waterfowl biologists’ libraries for it pulls together more information on the biology of the world’s 28 spp. of geese than can be found in any other reference work. Persons seeking information on goose biology including classification, ecology, reproduction, distribution, conservation, etc. now have a single work to use as a starting point. The book is not strong in its coverage of behavior. Usefulness of the book is tempered by overgeneralizations from species to species, and by lack of an adequate table of contents.

The state of goose literature has resulted in unequal species coverage with North American species strong on breeding biology while coverage of European species emphasizes winter biology. Asian species are poorly known in general. The author made a serious mistake in practically omitting coverage of the Hawaiian Goose (Branta sandvicensis), which he justified because of its uniqueness and a forthcoming monograph. I was disappointed that a more up to date review of Lesser Snow Goose (Chen caerulescens) biology was not included.

The book includes 16 color plates and numerous line drawings by Carol Ogilvie. Thirteen plates designed to aid identification of adult and immature geese are adequate but do not meet contemporary standards for ornithological illustration. The plate of downy young is poor. One additional plate dealing with aging/sexing is very useful. Pen and ink drawings lighten reading but do little to enhance the value of the book.

All in all this book will be a valuable addition to the library of waterfowl biologists and serious students of wild fowl. Its limited discussion of how our knowledge of geese relates to ornithology or science in general hamper its value. Nevertheless, Ogilvie has performed a valuable service in tackling a review of a group as large and complex as the geese of the world.—LEWIS W. ORING.

LORIES AND LORIKEETS. By Rosemary Low. Van Nostrand Reinhold Co., New York, 1977: 180 pp., 21 color plates, 1 table. $18.95.—Rosemary Low has not only provided a thorough and scholarly account of this subfamily of parrots, but has successfully bridged the gap between the interests of the aviculturist and the ornithologist. Her approach is particularly well suited to this group of birds, since much of what is known of their behavior and natural history has been provided by aviculturists. There is a paucity of field studies on lories, but because of their extraordinary beauty and entertaining dis-
positions, they have long been fancied by people who “keep parrots.” Thus the information in this book has come largely from her own experience or from records kept by other aviculturists over the last hundred years or so.

Six introductory chapters deal with the various general aspects of accommodation, feeding, and breeding of lories as well as their classification and natural history. Lest one be tempted to immediately rush out and buy some of these exquisite birds, Low cautions repeatedly regarding problems involved in their feeding and housing which are not encountered with other parrots. Her chapter on hand-rearing is an excellent summary of the various successful methods of carrying out this task. Several basic diets are discussed along with the techniques of administering them. In the chapter on their natural history an overview of the distribution, habitat preferences, and behavior of lories is given. Particular attention is given to what these parrots eat and how they ingest it. Low cites recent studies which indicate that this group, long believed to be nectar feeders, actually feed primarily on pollen, and their distinctive tongue is adapted for this end.

The author proceeds from this general account of the family to a discussion of each genus, species, and subspecies. Her classification follows that of Forshaw, except where she has indicated otherwise. No comment is made on his division of the order into three families, but apparently she does not follow this, since later she refers to the lories as belonging to the family Psittacidae. Although she has not attempted to resolve any systematic squabbles, Low does cite different points of view, where they exist. For example, it is almost certain that no one will ever really know how many subspecies of _Trichoglossus haematodus_ exist. Low has done a fine job of presenting all the available information on the matter, and at the end of the chapter on _Trichoglossus_, has organized it into a table. Correct or not, she succeeds in putting some order into what has always been regarded as one of the messiest problems in parrot systematics.

The book contains relatively few plates, but the descriptions of each form are detailed and well presented. Low has noted cases of even slight sexual dimorphism. Wherever possible, descriptions of immature birds are also given. One would probably have no difficulty in identifying any lory from these accounts, and the book will be held as a standard work for this, if for no other reason. General distributions are given along with altitude and habitat preferences. On the inside of the front cover is an outline map of Australia, Southeast Asia, and surrounding Pacific islands, with numbered localities. On the inside of the back cover is a list of these numbers and their corresponding localities. Beneath each locality are listed the lories which have been found there.

Low provides an extensive account of the avicultural history of each form described. When and by whom the bird was first imported, its price, and its present status in aviculture are recorded. Descriptions of behavior, particularly courtship displays and vocalizations, are given at an amateur’s level, but make interesting reading. Likewise, the occasional anecdotes are not so “petsy” that they would be likely to bore the purely scientific reader.

Breeding records are discussed in detail, particularly for the rarer species. Precise descriptions of the enclosures provided are given. Dates, climate preferences, clutch sizes, incubation periods, appearance of the young, and successful diets have all been included. In short, Low seems to have brought together any available information which would help one intending to breed the particular bird.

At a time when there is an increasing awareness of extinctions due to human encroachment, aviculture can no longer be considered only a hobby. People who are inclined
to keep pet birds should, if possible, attempt to breed them, and keep accurate records in doing so. Older works intended for use by parrot fanciers are heavily laced with charming anecdotes and contain little information of use to the present-day breeder. On the other hand, more recent presentations such as Forshaw (1973) lean toward the ornithologist’s point of view, dealing more with systematics and natural history than with practical pointers on breeding the birds in captivity. Low has taken a different direction and added a different dimension to previous accounts of lories and lorikeets.

I believe that this book will take a place among other standard works on parrots and I recommend it highly to anyone interested in the group, whatever be his reasons.—Susan L. Berman.


The Adventure of Birds. By Charlton Ogburn, illus. by Matthew Kalmenoff. William Morrow and Company, Inc., New York, 1976: 381 pp. $10.95.—Charlton Ogburn confesses that he has always had great admiration for the “qualities” of the kingbird. He finds that it “shows itself without restraint,” has energy that “brims over,” and inevitably favors a perch “from which it can command the scene” (p. 142). Ogburn indulges in considerable speculation about similarities between avian and human behavior; perhaps it is fitting, then, that his book displays the traits he imputes to one of his favorite birds. The Adventure of Birds exhibits an unrestrained and effusive prose style that often relies upon (self-acknowledged) clichés; it conveys the author’s boundless enthusiasm for his panoramic subject: birds in general.

This is a hybrid work, that tries to provide general information about birds, and in addition describes a personal philosophy about the pleasures of watching them. Ogburn is least successful in the first half of the book, “A World of Birds,” where he tries to combine his eclectic, digressive tone with a textbook exposition on basic features of avian physiology and behavior; he devotes much of this space to summarizing and quoting at length from a small core of standard references, for example Welty’s The Life of Birds. The information provided might be useful for a novice unaware of other sources. Because the organization of Ogburn’s book is idiosyncratic, many of the textual divisions seem intrusive; the headings read too much like predictable choices for headings in a book that has been written many times before: “The Domain of Birds,” “The Divisions of the Avian Treasure,” “Birds of Our Cultural Homeland,” etc. The second half of the book, “Birds Through the Year” is more successful, probably because Ogburn is not trying to describe what a bird is, and concentrates on transmitting to the reader the experience of birding, or simply being aware of birds through the different seasons. It is difficult not to appreciate the intensity of the author’s absorption, especially if the reader shares it, even remotely. Clearly, it is not fair to criticize Ogburn for not writing a more “ornithological” work; he admits at the start that he is an “ornithophile” and can well imagine what the reaction of an ornithologist might be to his lavishly subjective approach, and the baffling title of his book. Its appeal may be limited to those who enjoy energetic paeans to nature, and a great many besides a personal character. But instead of simply classifying Ogburn’s book as part of a genre aimed at a specific audience, it may be instructive to examine it more critically as a specimen of “nature-writing.”

Even consciously admitted indulgence has its dangers. Discussions of evolutionary processes are couched in anthropomorphic terms, for example, “Nature discovered”
and "Nature picked." This phraseology is used by an author who "knows better," but it is unfortunate that it is so common in books such as these, that try to be informative as well as personal, and are most likely to be read by the general public. The facile psychologizing often "permitted" in such writing leads to embarrassing and awkward analogies: "A Catbird from whose pillaged nest I once yanked a Black Snake broke into hurried song, as a Japanese, in a situation of tragedy, expressions of suffering blocked by a syndrome, may smile" (p. 101). Ogburn asserts that the creativity of humans and birds alike is "spurred by the exhilarations that spring from asserting one's being against the odds . . . ." (p. 127). He speculates about the differences in "drive" between various types of birds, and goes on to tell us, "it does seem that some human stocks, or social groups, and individuals do better than others at meeting new and challenging situations and are more aggressive" (p. 141). In speaking of bird territoriality, Ogburn provides us with an insight into his own political view of nature. A bird defending its territory is a "communicant of the Universal" and "dispatches the enemies of the rightful order—he, the warrior, the elect," who is "possessed by the spirit" (p. 147). Citing sociobiological theory, Ogburn remarks that a human's territorial impulse "would appear to be in his blood, and I cannot see that it has been much diluted, if any" (p. 151). There are even more facile ruminations: "It may be that the great apes, second only to man in intelligence, have made so little of their opportunities on earth, because like some human tribes and many, if not most, human individuals, they lack the need for exotic fulfillments" (p. 188).

What is Ogburn's ultimate message? In a bird's cry, he finds something that is elusive: "If it is not in the bird itself, a rendering—largely unconscious, admittedly—of what is in the very plasma of life, derived from who knows where, then, to me, it is a quality of the cosmos of which the bird is the—again, largely unconscious—agency of expression" (p. 368). Like many nature-writers, he harbors the almost religious hope that there will always be more to the natural world than we can comprehend. By trying to be panoramically informative and anecdotal at the same time, Ogburn has exhibited some of the pitfalls of the genre he has chosen. Perhaps there is a slimmer volume hidden within this one, that, being more modest in scope, would have been more successful.—Kathleen E. Duffin.


The Birds of Malaŵi. By C. W. Benson and F. M. Benson. Sponsored by D. W. K. Macpherson and printed by the Mountfort Press, Limbe, Malaŵi, 1977: 263 pp., 1 color plate, 1 map, soft covers. Obtainable from Hon. Secretary, National Fauna Preservation Society of Malaŵi, P.O. Box 5135, Limbe, Malaŵi, for Kwachas 5.00 ($7.00) surface mail (transit as much as six months) or K 8.15 ($11.40) air mail.—The Bensons have written a scholarly and useful list of birds of Malaŵi, an easily visited African country with little-visited national parks, a large Rift Valley lake, and 620 species of birds. The scope of the book is like that of The Birds of Zambia by Benson et al. The text gives a systematic list of species, with notes on local distribution, habitat, food, resident or migratory status, dates of breeding, clutch size, and numbers to published references. The previous list of birds for this area, A Check List of the Birds of Nyasaland, was published in 1953 by C. W. Benson, and the present book brings our knowledge of the birds up to date. Few species have been added to the list since that time, but considerable
field work by Benson and others in Malawi and its neighboring countries has contributed to the comments on the ecology of the species.

An introduction explains the abbreviated style of the sections on breeding and the references, and it describes the habitats found in Malawi. Breeding data are fewer than for Zambia, and the authors often refer to breeding dates of Zambia or Rhodesia. The species accounts point out room for future field studies on ecological differences among related species and on some surprising apparent gaps in knowledge of basic breeding biology. No local nestings are known of several Egretta species (including Cattle Egret) or of Ardeola ralloides, all widespread African herons. The detail and attention given each species match that of the companion Zambian book. Appendixes include notes on museum collections of birds of Malawi (more than 16,000 specimens), useful particularly as 71 species and subspecies of birds were first described from Malawi. A gazetteer of localities, together with a synonymy of the changing place names, and a map, helps the reader locate places mentioned in the text. An appendix of 10 pages gives distributional and other notes on certain species. G. Harrison adds a section on recoveries of ringed birds, with only one bird ringed in Malawi recovered abroad, 6 species ringed in other countries and recovered in Malawi, and 5 Palearctic migrants and one intra-African migrant retrapped at the same locality in successive nonbreeding seasons (these last by D. B. Hamner). An index is included to both scientific and English names of species. F. M. Benson has painted an attractive color plate of the White-winged Apalis (Apalis chartiessa macphersoni), one of the birds whose distribution is restricted in Malawi to forest habitat.

The Bensons have written a thorough book on the distribution of the birds of Malawi, and may we hope that the book helps promote an appreciation of the remarkable diversity of life of that country.—Robert B. Payne.


Roberts Birds of South Africa. Fourth Edition. By G. R. McLachlan and R. Liversidge. Trustees of the John Voecker Bird Book Fund, 5 Church Square, Cape Town, South Africa: xxxii and 660 pp., 72 color plates, numerous marginal sketches and distributional maps. South African Rand 12 (about $15).—The publication of Austin Roberts' Birds of South Africa in 1940 established the landmark for handbooks of African birds. Since that time others have been published, but none have matched the combination of fine color plates, concise format, and informative text. The present edition of Roberts differs from the third, published in 1970, by a complete rearrangement of color plates, a picturing in color of nearly all southern African birds, and an updating of the species accounts and local distribution.

The text includes for each species names (scientific, English, Afrikaans, and sometimes local African), identification marks, comparison with similar species, distribution in southern Africa (here, South-West Africa and the entire area south of the Zambezi River), habitat, behavior, food, voice, and breeding, including nest, eggs, breeding season, and incubation and fledging times. Subspecies occurring within southern Africa are described briefly. For most species the accounts are identical to those of the previous edition, but are new for species included since that time. These accounts give useful and reliable information about the natural history of the species, and the new Roberts should serve well in pointing out what basic information is lacking.

The major change from earlier editions is in the illustrations. Most of the color plates
of N. C. K. Lighton are retained from the first edition, but here they are larger. Lighton’s figures had suffered from over-reduction, and the new format shows his work to better advantage. The result is more pleasing to the eye, though the colors, notably the blues and greens, are rather washed out (for example in the Blue Waxbills and Melba Finches). In addition, K. Newman has illustrated 31 new color plates. Newman’s illustrations go well with Lighton’s but are more sketchy, showing bold plumage patterns rather than feather detail, and are better suited for field identification. New plates include the water birds, hawks and eagles in flight, hawks and eagles perched, francolins, waders, plovers, gulls and terns at rest and in flight, larks, and some Cisticola species. These replace all the black and white plates and the less satisfactory color plates of the earlier editions. Newman also has added a few species not included in Lighton’s color plates, mainly species added to the southern African list since the first edition of Roberts, introduced species, and a few additional plumages such as female Cuckoo-finch Anomalospiza imberbis.

Illustrations in the wide margins are another new and attractive feature of the book. Some old illustrations by H. Grönvold are reprinted from Stark and Sclater’s Fauna of South Africa: Birds, and some new figures are drawn by Jill Adams. The marginal figures include flight field marks of storm petrels (the only group not illustrated in color), prion bills, downy young of some species of grebes, ducks, coursers, sandplovers, and a bustard, heads of some raptors, flight feathers of terns, wing patterns of nightjars, wings and tails of some Cisticola species, and nests of some weavers.

The introduction has the same comments on classification, bibliography, ornithological history, and habitat regions as the two previous editions. The family accounts include technical details of taxonomy and anatomy not in the earlier editions, but omit some natural history information, unfortunately for a field book. The index lists separately the species by English, scientific, and Afrikaans names.

The book is the best available both as a field guide and a concise compendium of natural history of birds for any region of Africa. As the earlier editions have sold over 100,000 copies, and the new edition is an improvement in illustrations over those, the new Roberts is certain to be the new standard for African field ornithologists. I recommend it to everyone with an interest in African birds.—ROBERT B. PAYNE.
It has been customary for people interested in birds to name their publications after a bird species that for some reason is of special interest or significance. This practice is world wide in application and not just confined to avian publications in North America. Although there are some highly respected journals bearing such titles, I often wonder whether these titles have the same connotation of respectability to others that they do to ornithologists. I think this is an important matter to consider and I would enjoy learning the views of others on the subject. For example, should long standing bird journal names be changed to titles that more appropriately reflect journal contents? Obviously our journal, *The Wilson Bulletin*, does not have a bird-name title even though the cover characteristically shows a Wilson’s Warbler. So it is reasonable to ask why this matter should be brought up in the pages of the *Bulletin*. My response is that I think our journal name may be even more ambiguous to the outsider, and certainly just as puzzling, as a journal named after a particular bird. It would be more explicit for example if there were an ornithological journal titled *American Journal of Ornithology* just as there is an *American Journal of Botany, . . . Physics, . . . Physiology*, etc.

Is it important to “impress” others by having a scholarly sounding journal title? Perhaps not in earlier times when only students of birds were interested in their journals. The present interdisciplinary trends in science have changed this significantly and now scientists from other areas of biology are becoming aware of ornithological journals. Even more importantly, administrators at colleges and universities increasingly are stressing the need for good publication records in forming recommendations on tenure, promotion, and salary raises for faculty members. Three decades ago when so-called amateurs were most conspicuous in The Wilson Ornithological Society this policy would not have affected Society members much. Since then, however, there has been a steady increase in the number of professional ornithologists active in the Society. These members do indeed care about tenure, promotion, and salary and hope that administrators will be duly impressed with their publications in bird journals, including *The Wilson Bulletin*.

An issue of this kind has confronted the Society before. For example, I remember when the Society was called the *Wilson Ornithological Club*. Maurice Brooks described in his talk at the annual meeting last May in West Virginia how the term *Society* was adopted to impress the Internal Revenue Service with the desirability of accepting income tax deductions claimed by members for annual meeting expenses. I remember too, comments at the time about how the name change was needed to impress college administration with the fact that we really were a scientific *Society*, not just a social *Club*, and thus were worthy of official sanction for faculty attendance at meetings.

Returning to the issue at hand, I would like to know how members feel on the subject of changing the name of *The Wilson Bulletin* to a title that is more obviously ornithological. I would enjoy receiving these comments prior to the next annual meeting, which will be in early April in Omaha, Nebraska. This will provide a basis for discussion of the issue by the Executive Council of the Society when it convenes there. I should emphasize that no immediate action on the matter is anticipated. Instead, there simply will be an informational session for appraising current feelings on the subject.

I’ve compiled a list of 9 possible journal names that could be more explicit for an American journal devoted to ornithology. Some of these titles are *American Journal of Ornithology*, or just *American Ornithology*, or perhaps *Journal of Ornithology*. The simplest is *Ornithology* (comparable to *Ecology*), the most complex, *Journal of the Wilson Ornithological Society*. I notice in the recent final report for the Workshop on a National Plan for Ornithology (supported by NSF) that an urgent need was identified.
for having a new journal devoted entirely to avian ecology. Perhaps the Bulletin could satisfy some of this need by stressing ecology exclusively, which it now emphasizes, and becoming the Journal of Avian Ecology.

As a final comment I should point out that the Bulletin did not always bear its present name. At one time in its early years it was called The Semi-Annual. By this precedent the present volumes should be called The Quarterly, hardly ornithological, hardly impressive.—DOUGLAS JAMES.

ORNITHOLOGICAL NEWS

LOUIS AGASSIZ FUERTES AND MARGARET MORSE NICE AWARDS

Fuertes Awards are devoted to the encouragement and stimulation of young ornithologists. One particular desire is the development of research interests among amateur ornithologists and students. Any kind of ornithological research may be aided. Recipients of grants need not be associated with academic institutions. Each proposal is considered primarily on the basis of possible contributions to ornithological knowledge. Although grantees are not required to publish their studies in The Wilson Bulletin, it is hoped that they will submit their manuscripts to the editor of The Wilson Bulletin for consideration.

Most statements applicable to the Fuertes Awards also are applicable to the Nice Award. However, the Nice Award is limited to applicants not associated with a college or university. It is intended to encourage the independent researcher without access to funds and facilities generally available at the colleges. High school students are eligible. In some years 2 Fuertes Awards have been made, in some years only one. Amount given is $200.00 per award. One Nice Award is made annually in the amount of $200.00. Interested persons may write to Clait E. Braun, Wildlife Research Center, P.O. Box 2287, Fort Collins, Colorado 80522. Completed applications must be received by 1 March 1979. Final decisions will be made by the Council of The Wilson Ornithological Society at the annual meeting of the Society, 5-8 April 1979.

PAUL A. STEWART AWARDS

The Paul A. Stewart Fund for Ornithological Research has been established by donations from Paul A. Stewart. Income from this endowment will be awarded annually to support research in ornithology especially studies of bird movements based on banding and analyses of recoveries and returns and investigations pertaining to economic ornithology. Several Stewart Awards in the amount of $200.00 each will be available each year. Stewart Awards will be equally available to students, amateurs, and professionals. Interested persons may write to Clait E. Braun, Wildlife Research Center, P.O. Box 2287, Fort Collins, Colorado 80522. Completed applications must be received by 1 March 1979. Final decisions will be made by the Council of The Wilson Ornithological Society at the annual meeting of the Society, 5-8 April 1979.
1979 ANNUAL MEETING OF THE WILSON ORNITHOLOGICAL SOCIETY

The 60th Annual meeting of the Wilson Ornithological Society will be held in Omaha, Nebraska on 5-8 April 1979. The meeting will be hosted by the University of Nebraska at Omaha and by the Nebraska Ornithologists' Union.

A special feature of the meeting will be a symposium titled “The Biology of Bird Species with Limited Distribution.” The symposium is being organized by Drs. Abbot Gaunt and Jon Barlow.

Planned field trips include visits to waterfowl concentrations along the Missouri River bottoms, a trip to the Central Platte River to view Sandhill Cranes, and a visit to a prairie chicken booming ground.

The chairman of the local committee is Dr. Roger Sharpe, Department of Biology, University of Nebraska at Omaha, 68182.

SALE OF JACK-PINE WARBLER BACK ISSUES

As a service to ornithologists wishing to build or improve their libraries (either personal or institutional), The Jack-Pine Warbler is having a one-time sale of back issues. The sale will end 15 April 1979. There are 2 options: (1) You may purchase 1 copy of every available back issue from 1928 (The Jack-Pine Warbler began publication in 1926) to 1977 for $15.00 plus postage. At the time of this writing, this includes 168 issues beginning with Fall 1928 and complete volumes from 1938 to 1977 with the exception of 1951-1954 (6 issues exhausted). Twenty issues, however, are represented by fewer than 10 copies (these are mostly prior to 1938 and between 1950 and 1954). Sets will be assembled on a first come, first served basis; later orders will receive fewer issues. If stocks are depleted below 125 issues, prospective purchasers will be notified. (2) Individual issues (1927-1977) may be purchased for 20 cents apiece with a $1.00 minimum (postage extra).

Regular prices are $.50-1.00 per issue 1928-1976 and $2.50 1977-1978. Either plan, consequently, offers substantial savings. Single copy sale prices are all below one-half price. Maximum savings, however, are available on sets; early purchasers will be saving more than $70.00 per set and later purchasers only slightly less. Order from Michigan Audubon Society Bookshop, 7000 North Westnedge, Kalamazoo, MI 49001. You will be billed.

ERRATUM

In the paper by William Post in the June 1978 Wilson Bulletin (Social and foraging behavior of warblers wintering in Puerto Rican coastal scrub. Wilson Bull. 90:197–214), the references to the Bahama Yellowthroat on pages 198 and 199 should be references to the Common Yellowthroat (Geothlypis trichas).
WOS COMMITTEE CHAIRMEN

President Douglas James has appointed the following to chair the WOS committees for 1978-1979:

Auditing Committee, to be selected by Ernest Hoover as has been customary for the past several years so that the audit can be conducted prior to the 1979 meeting.
Conservation Committee, Eric G. Bolen
Endowment Committee, Don Bleitz
Ernest P. Edwards Prizes, Jerome A. Jackson
International Council for Bird Preservation Representative, Helen S. Lapham
Investment Trustees Committee, Philips B. Street
Library Committee, William A. Lunk
Local Committee for 1979 Meeting, Roger Sharpe, Department of Zoology, University of Nebraska, Omaha, Nebraska
Louis Agassiz Fuertes, Margaret M. Nice, and Paul Stewart Awards, Clait E. Braun
Membership Committee, Robert C. Whitmore
Nominating Committee, Sidney A. Gauthreaux
Projected Budget Committee, Horace H. Jeter
Standing Resolutions Committee, Robert L. Burns
Student Membership Committee, James R. Karr

VULTURE SYMPOSIUM

An International Symposium on the Vultures, sponsored by the Western Foundation of Vertebrate Zoology, will be held 23-26 March 1979, at the Santa Barbara Museum of Natural History, Santa Barbara, California. Papers on any aspect of life history, behavior, or conservation of both Old World and New World vultures are solicited. For further information, contact: Mr. Sanford R. Wilbur, c/o U.S. Fish and Wildlife Service, 1190 E. Ojai Avenue, Ojai, CA 93023 (Phone 805/646-5455).

FRANK M. CHAPMAN FUND

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