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The **XIX International Ornithological Congress** will be held in Ottawa, Canada, from **22 to 29 June 1986.** Prof. Dr. Klaus Immelmann is President. The scientific program will include plenary lectures, symposia, contributed papers (oral and posters), round-table discussions, special-interest group meetings, and workshops. Pre- and post-congress excursions and workshops are planned, as well as early morning bird walks and other activities for members and accompanying members. The deadline for registration and submission of contributed papers is **January 1986.** Additional information, the final circular, and registration forms are available from: **Dr. Henri Ouellet, Secretary General, XIX Congressus Internationalis Ornithologicus, National Museum of Natural Sciences, Ottawa, Ontario K1A 0M8, Canada.**

THE REGULATION OF EGG TEMPERATURES AND ATTENTIVENESS PATTERNS IN THE DUSKY FLYCATCHER (*EMPIDONAX OBERHOLSERI*)

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ABSTRACT.—Egg temperatures (T_{egg}) and attentiveness were measured in *Empidonax oberholseri* breeding at high altitude in the Sierra Nevada of California. Eggs were tended in daytime during the laying period but were above the assumed threshold temperature for development (28°C) for only 17.6% of the time. Mean T_{egg} increased during the laying period and for the first few days of incubation. This may have been related to brood patch development.

Full-time incubation began at night following the laying of the penultimate (6 cases) or prepenultimate egg (3 cases). Once incubation began, there was little diurnal variation in mean T_{egg}. Eggs were above developmental threshold for 92.2% of the time during the active day and 99.9% of the time during night rest. Mean T_{egg} for 5 nests for the full period of incubation was 37.62°C.

Trends in T_{egg} indicated that body temperature (T_b) of incubating females decreased at night when ambient temperature (T_a) was between 12°C and 4°C. Shivering thermogenesis probably was employed at T_as below 4°C.

During storms, despite heavy hail and rain, females endured on the nest for long periods. If the storm continued, they eventually left to feed, thus exposing eggs to possible damage. When potent thermolytic conditions were coupled with food shortage, as during large storms or prolonged episodes of cold, windy weather, incubating females neglected their eggs in order to extend foraging time. They also allowed eggs to cool at night by withdrawing their brood patch. We assume that this increased their ability to defend T_b.

Attentiveness varied diurnally, being highest at midday. Duration of foraging trips varied little with time of day or T_a, but attentive bouts were longest at midday. The rate of foraging bouts was highest at the beginning and end of the active day. Unlike many species, total attentiveness in *E. oberholseri* was correlated positively with T_a. This may be a general pattern in open-nesting birds at high altitude that has evolved because of the need to protect eggs from damage by solar radiation. Repeated excursions of eggs to low temperatures or outright periods of neglect during cold weather did not seem to affect embryo survival. *Received 10 April 1984, accepted 2 October 1984.*

STRATEGIES employed by incubating birds must often represent compromises between the embryo's thermal requirements for development and the tending adult's energy balance (White and Kinney 1974, Carey 1980a, Vleck 1981a). It follows that information on egg temperatures and on attentiveness patterns of adults during incubation should elucidate important elements of these coadapted characters, particularly when they are being amplified by stringent environmental conditions.

To learn more about how the scope and mechanisms of adaptation to the environment are expressed during incubation, we studied the Dusky Flycatcher (*Empidonax oberholseri*) at a high-altitude location where periods of inclement weather often occur. This small (11-g) bird builds an open nest, and only the female incubates. It winters in Mexico and summers in the western United States and far-western Canada (Johnson 1963). In California it generally breeds in montane habitat between elevations of 1,500 and 3,000 m.

STUDY AREA AND METHODS

Our study area is at about 3,000 m in the eastern Sierra Nevada near Tioga Pass, Mono County, California. The area consists mostly of the upper portions of glaciated valleys that have lakes, wet meadows, willows (*Salix* spp.), and small pines (*Pinus jeffreyi* and *P. contorta*) in their bottoms and quaking aspens (*Populus tremuloides*), tall pines, and talus on their sides. The majority of nests (n = 110) were located in willows, aspens, or pines between 1 and 4 m above the ground. Clutches were started during June and July, and clutch size usually was 3 or 4. Freshly laid eggs

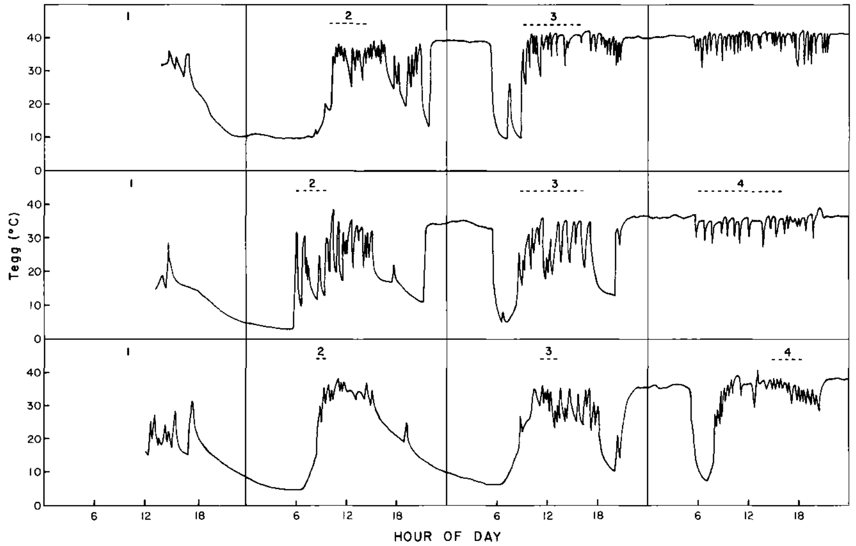

Fig. 1. Egg temperatures in *Empidonax oberholseri* during the laying period in 1 three-egg (top) and 2 four-egg clutches (middle and bottom). Each box is a 24-h period. Recordings were made from a thermocouple inserted into the first egg on the day it was laid. Known boundaries for laying times of subsequent eggs are indicated by dashed lines under the egg's number.

weighed about 1.2 g. Data were gathered during the summers of 1981, 1982, and 1983.

Egg temperature (T_{egg}) was measured using a 40-gauge copper-constantan thermocouple that was inserted to the egg center, spot-glued to the shell, threaded through the bottom of the nest, and connected to a Bailey thermometer (Bat-12). An Esterline-Angus strip chart recorder (MS411BB) provided a continuous record. Egg temperatures used in this report were taken from these charts at 3-min intervals. Attentiveness was determined from the same records because sudden temperature changes usually signaled departure or arrival of the incubating female. This was verified by direct observation. Thermocouples were inserted in the first eggs laid in 11 *E. oberholseri* nests. Two of these nests were depredated within 48 h, but data were obtained for the complete laying period on all 9 of the remaining clutches. One of these was lost during incubation, and we report here attentiveness data from the remaining 8 clutches. Temperature calibration difficulties were encountered at times in 3 nests, so T_{egg} data for the whole incubation period are presented only for 5 nests. Ambient temperature (T_a) was recorded with hygrothermographs placed 1-4 m from the nest or from thermocouples placed immediately beneath the bottom of the nest.

Brood-patch temperatures were taken with a custom-built surface probe and thermometer (Bailey, Bat-12). Incubating females were often so docile that they would permit us to slip the probe under them and hold it against their brood patch while they sat on the nest. Sunrise and sunset times were obtained by direct observation of the sun's appearance and disappearance at the study area. Pacific Daylight Time was used throughout.

We defined night rest as the period between the return of the female to the nest for the last time in the evening until she left the next morning. The active day was the time between periods of night rest. The egg-laying period began with the laying of the first egg and ended with the onset of incubation. Incubation began when the female sat on the eggs continuously at night for the first time.

RESULTS

Temperatures during egg-laying.—Temperature recordings of the first egg in a clutch began on the day it was laid. This provided a record of T_{egg} and attentiveness for both laying and incubation periods. Data were obtained for the complete laying period in 3 three-egg clutches and 6 four-egg clutches. The development of incubation was similar in all three-egg clutches in that females tended eggs during the day and began nighttime sitting just prior to laying the third egg (Fig. 1, top). Two patterns were observed in four-egg clutches. In 3 nests nighttime sitting began before the third egg was laid (Fig. 1, middle), and in the other 3 it began before the fourth egg was laid (Fig. 1, bottom).

TABLE 1. Mean 24-h egg temperatures (°C) in *Empidonax oberholseri* during the laying period and during incubation. Data are from 5 nests. *n* refers to individual readings taken at 3-min intervals.

Day	Mean	SD	*n*
Laying			
1	14.7	5.9	928
2	16.3	10.6	1,920
3	20.3	10.7	480
Incubation			
1	34.0	8.6	2,336
2	36.7	4.4	2,100
3	37.8	2.6	2,201
4	37.6	7.2	2,400
5	38.3	6.1	2,400
6	38.8	2.2	2,400
7	38.6	2.2	1,883
8	38.5	2.5	2,160
9	38.2	2.3	2,400
10	37.4	3.8	2,280
11	37.6	3.3	2,220
12	37.7	4.9	2,313
13	37.8	2.5	2,400
14	37.8	2.6	2,325
15	37.7	2.8	1,020

TABLE 2. Mean egg temperature (°C) during constant attentiveness (following 15 min or more of continuous sitting) by day of incubation in *Empidonax oberholseri* during the active day and during night rest. Data are from 5 nests. *n* refers to individual readings taken at 3-min intervals.

Day of incubation	Active day			Night rest		
	Mean	SD	*n*	Mean	SD	*n*
1	34.4	8.1	360	36.0	2.9	531
2	37.3	3.4	525	36.9	2.8	804
3	37.8	2.6	479	37.7	2.1	804
4	38.4	2.5	605	38.4	1.7	796
5	38.0	2.4	447	38.0	2.7	829
6	39.0	2.0	592	38.4	2.0	887
7	39.6	1.5	672	39.2	1.6	868
8	39.8	1.5	423	38.7	1.6	690
9	39.7	1.5	458	39.2	1.8	773
10	39.1	1.6	488	38.7	1.9	893
11	38.4	1.7	535	38.4	1.9	856
12	38.4	1.7	504	38.9	1.7	781
13	38.9	2.2	533	38.2	1.8	815
14	38.7	1.7	508	38.0	1.6	890
15	38.7	1.8	530	38.2	1.8	821

Mean T_{egg} rose steadily during the laying period and continued to increase through the first few days of incubation (Table 1). T_{egg} was lowest on the first night of incubation and tended to increase slightly but steadily for several consecutive nights thereafter. Mean T_{egg} during episodes of constant attentiveness (defined as periods when the female was on for at least 15 min and T_{egg} was at equilibrium) rose 4.0°C for active day measurements and 2.4°C for night rest during the first four days of incubation (Table 2). Both increases were significant (t-test, $P < 0.01$ in each case) and may be related to brood-patch development. Mean brood-patch temperature of 2 females between days 1 and 4 of incubation was 41.52°C (SD = 0.56°C, $n = 5$). Mean patch temperature of 3 females taken between days 6 and 15 of incubation was 42.44°C (SD = 0.52°C, $n = 10$). These means were different (t-test, $P < 0.05$). Tightness of sit also could be involved in T_{egg} changes with progress of incubation, but we have no way to evaluate this possibility.

The first night of incubation, unlike subsequent nights, was bracketed by long inattentive periods in all 9 nests studied (see Fig. 1). Mean duration of the inattentive bout was 58.9 min (SD = 69.4 min) immediately preceding and 89.6 min (SD = 49.5 min) following the first night of sitting. These periods off were much longer than those observed before and after all other nights of incubation (before = 4.4 ± 1.4 min, after = 4.9 ± 0.6 min). It appears that females were both anticipating and reacting to the first night of incubation with very long foraging bouts.

Examination of T_{egg} records gives the impression that *E. oberholseri* spend considerable time on their nests during the laying period (Fig. 1). Eggs were allowed to assume ambient temperatures at night but from the first egg onward were tended regularly in daytime. Despite the frequent daytime visits of females, however, eggs were not maintained for long periods at temperatures necessary for embryonic growth (Table 3).

We cannot yet report conclusively on the time of day that eggs are laid. We do know that laying can occur anywhere from early morning to midafternoon, and we suspect that the pattern observed in Fig. 1 (bottom) is common, i.e. consecutive eggs are laid at intervals greater than 24 h.

Temperatures during incubation.—Upon completion of the clutch, eggs were tended steadily with short interruptions during daylight hours when females left to forage. The duration of foraging bouts varied little unless it was stormy or windy (see below). This rather constant at-

TABLE 3. Percent of time spent by *Epidonax oberholseri* eggs within various temperature intervals during laying and during incubation. Data are from 5 nests.

Temperature interval (°C)	Laying period	Incubation: Active day	Incubation: Night rest
0.0-1.9	0.00	0.19	0.00
2.0-3.9	1.35	0.28	0.00
4.0-5.9	9.90	0.33	0.00
6.0-7.9	11.53	0.59	0.00
8.0-9.9	9.00	0.97	0.00
10.0-11.9	9.72	1.03	0.00
12.0-13.9	8.07	0.80	0.00
14.0-15.9	6.33	0.34	0.00
16.0-17.9	6.66	0.44	0.00
18.0-19.9	4.41	0.43	0.00
20.0-21.9	5.25	0.53	0.01
22.0-23.9	3.09	0.47	0.01
24.0-25.9	3.78	0.70	0.02
26.0-27.9	3.27	0.66	0.04
28.0-29.9	3.33	1.23	0.20
30.0-31.9	3.27	2.44	0.56
32.0-33.9	3.66	5.33	1.60
34.0-35.9	5.13	11.95	4.79
36.0-37.9	1.59	22.01	36.00
38.0-39.9	0.45	23.23	25.54
40.0-41.9	0.12	23.37	30.02
42.0-43.9	0.09	2.60	1.21
44.0-45.9	0.00	0.08	0.00

tention yielded mean values for T_{egg} that had little diurnal variation. The lowest means occurred in early morning, when foraging coincided with the day's lowest T_as (Fig. 2). The grand mean for T_{egg} measured every 3 min in 5 nests for the full period of incubation was 37.62°C (SD = 3.97°C, $n = 32{,}838$).

T_{egg} might be expected to vary more in daytime than at night because of foraging trips by tending females and because of greater variability in thermal conditions during daylight hours. This expectation is met when the relative distributions of T_{egg} during the active day and during night rest are examined (Table 3). Daytime T_{egg} had a range twice that measured at night. In both time frames, however T_{egg} was most frequently in the range of 36-42°C (68.6% of the time during the active day and 91.6% during night rest). Eggs were above 28°C for 92.2% of the time in the daytime and 99.9% of the time at night (Table 3).

Large variations did not occur in T_{egg} during night rest, but a consistent and interesting relationship between nighttime T_{egg} and T_a was present nonetheless (Fig. 3). Mean T_{egg} decreased steadily at T_as between 12°C and 4°C, then increased to a level seen at the higher T_as. The total change in mean T_{egg} was only 2.4°C (37.3-39.7°C), but the sample sizes involved were large and all consecutive pairs of means between 0°C and 14°C were significantly different from one another (t-test, $P < 0.01$ in every case).

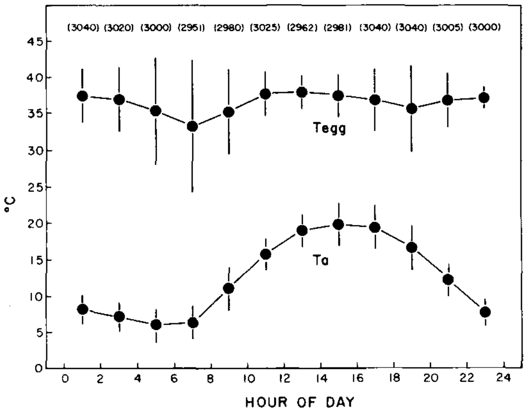

Fig. 2. Mean egg (T_{egg}) and air (T_a) temperatures per 2-h interval for all days of incubation in *Empidonax oberholseri*. Vertical lines show ±1 SD. Sample sizes are in parentheses. Temperatures were taken every 3 min from 5 nests.

Some of our most informative incubating bird-environment interactions are revealed in individual records obtained during environmental perturbations. In Fig. 4 are plotted 72 consecutive hours of T_{egg} recordings (direct tracings of the original records, 25-27 July 1982, days 11-13 of incubation) along with concur-

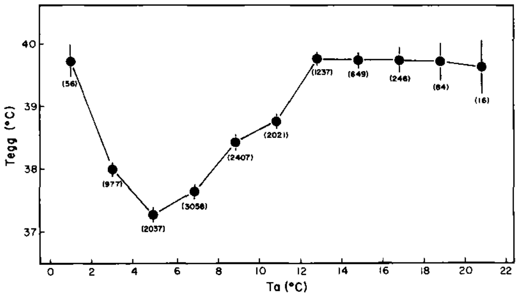

Fig. 3. Relationship of mean egg temperature (T_{egg}) to air temperature (T_a) during night rest in *Empidonax oberholseri*. Vertical lines show ±2 SE. Sample sizes are in parentheses. Temperatures were taken every 3 min from 5 nests.

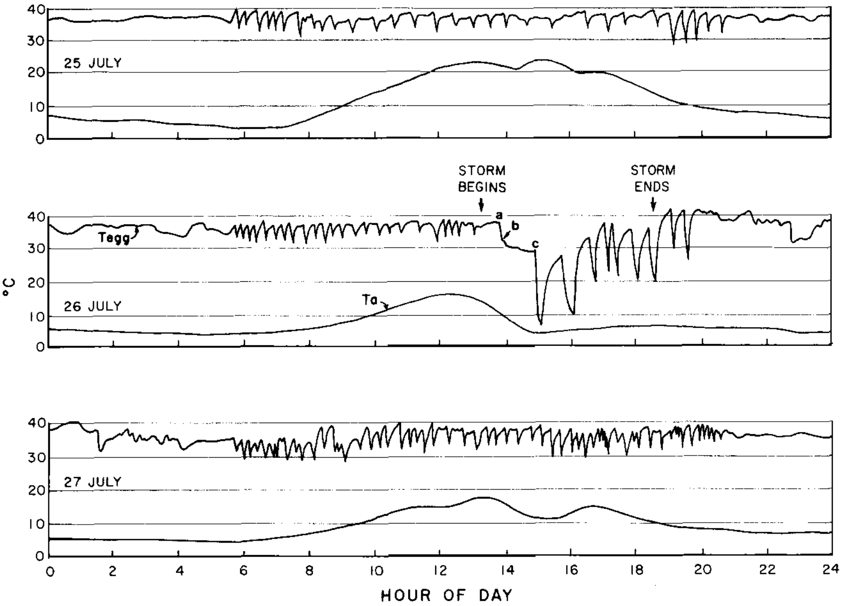

Fig. 4. Egg (T_{egg}) and air (T_a) temperatures for 3 consecutive days at nest 15. A severe storm, marked by arrows, occurred on 26 July (middle).

rent data on T_a. This nest (#15) was located 1.5 m above the ground in a willow. It contained 4 eggs, 2 of which were implanted with thermocouples. One of the 2 undisturbed eggs hatched, and the nestling eventually fledged. For all of 25 July (Fig. 4, top) and until about noon on 26 July (Fig. 4, middle) weather conditions were mild, and the patterns of T_{egg} and attentiveness shown are typical for those of fair weather. The sky then became overcast, and at 1314 a downfall of hail began. Hail and then rain continued until 1830, at which time hailstones were on the ground to a depth of 2 cm. Several *E. oberholseri* and Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) nestlings were killed by this storm, and many *E. oberholseri* eggs were heavily dented by impact from hailstones. This type of damage could occur only if the female left the nest while the storm was in progress. At nest 15 the T_{egg} record shows (Fig. 4, middle) that the female remained on the nest continuously for the first 31 min of the storm, then got off (point a) for 6 min. She returned (point b) and sat for 62 min before getting off again (point c). Although this was a long attentive period, T_{egg} was only about 30°C throughout. We think the female was unable to heat the eggs higher than this because hailstones accumulated in the nest during the interval a-b. At point c she began a series of foraging trips during which T_{egg} dropped precipitously. Seven such trips were made while the storm was still in progress, and 9 trips were made in all before she began night rest. These trips lasted from 4 to 22 min, with a mean of 9.7 min (SD = 5.3). Eggs took much longer to rewarm than to cool even though they were not always rewarmed completely. Attentive bouts varied between 10 and 39 min (mean = 25.4, SD = 9.9, $n = 8$). Note that the female began night rest about 80 min earlier than was customary for her and that T_{egg} variation was greater than usual during night rest. The latter probably occurred because the nest was water-soaked.

During the next active day (27 July) this female made 58 foraging bouts, in contrast to only 30 trips made on 25 July. This increased rate of feeding may have been an attempt to compensate for an energy deficit suffered the previous day and/or a reaction to lower than usual T_as on the 27th.

High winds, particularly when coupled with low T_as, are another environmental circumstance with energetic consequences to incubating *E. oberholseri*. A 72-h tracing of temperatures at nest 8 on 7-9 July 1983, days 10-12 of incubation, is illustrative (Fig. 5). This nest was

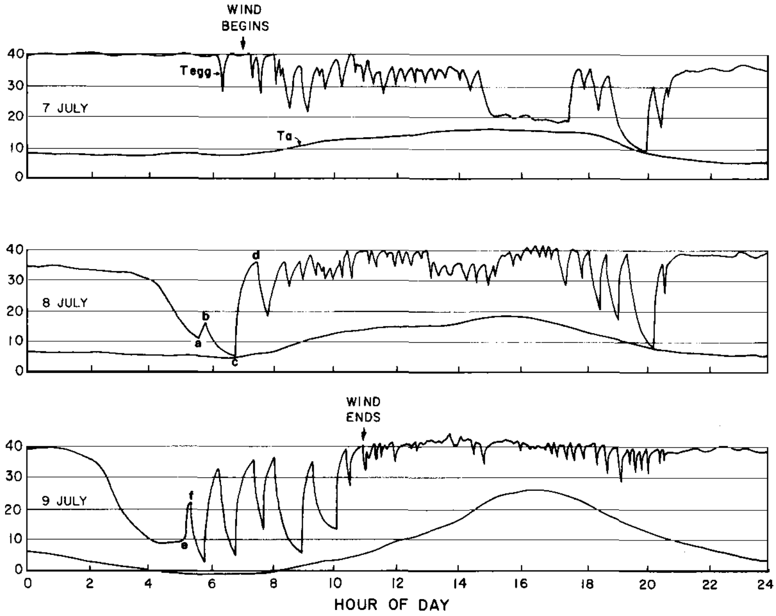

Fig. 5. Egg (T_{egg}) and air (T_a) temperatures for 3 consecutive days at nest 8. Strong winds began on 7 July (top) and continued until 9 July (bottom).

located 0.6 m above the ground in a stunted aspen on the upper portion of a talus slope. This was an unusually open and exposed nesting site. High winds began blowing on the study area ca. 0700 on 7 July 1983 and continued day and night until ca. 1100 on 9 July. We did not have wind-recording instruments but believe that wind speeds, conservatively, were 10–20 m/s during most of this 52-h span. The female at nest 8 was off her eggs for long periods of time, especially at the beginning and end of the active day. T_{egg} dropped to near ambient levels (which generally were low) during several of these trips. The longest period off (175 min) occurred in the afternoon of 7 July. T_{egg} remained 4–5°C above T_a during this particular bout because the eggs were heated somewhat by the sun. The lowest T_{egg} recorded during an off bout was 2.8°C at 0550 on 9 July.

In the last hours of night rest on 8 July (Fig. 5, middle), T_{egg} decreased steadily until at 0536 it reached 11.1°C (point a). During the next 11 min (a–b), T_{egg} increased to 16.4°C. It then decreased during the next 57 min (b–c) to 5.0°C. Our interpretation of this record is that the female reduced or eliminated contact between her brood patch and eggs during the last hours of night rest. Contact was reestablished briefly (a–b), whereupon she began the day's first foraging trip. During the first attentive period of the active day (c–d) full contact with eggs occurred, and they were reheated to the usual level.

During the next night (Fig. 5, bottom) this cycle of events was repeated. As before, T_{egg} decreased rapidly, but it then leveled off and was maintained well above T_a at between 8.2 and 9.9°C for 71 min. Then between 0512 (point e) and 0523 (point f) T_{egg} increased from 9.9 to 21.7°C. Again, this female seemed deliberately to reduce heat flow to her eggs. They were allowed to remain cool and were rewarmed (e–f) just before onset (point f) of the day's first foraging trip.

We obtained one additional record from another nest wherein the pattern in T_{egg} was similar to that observed in nest 8. The only unusual associated environmental circumstances were thundershowers during the two days preceding the response. We can only infer the female's actions from T_{egg} records in these cases, but similar tracings were obtained from Goldcrests (*Regulus regulus*) standing or roosting over eggs at night during the laying period (Haftorn 1978a). Decreased body temperature (T_b) in the female at nest 8 also could have contributed to

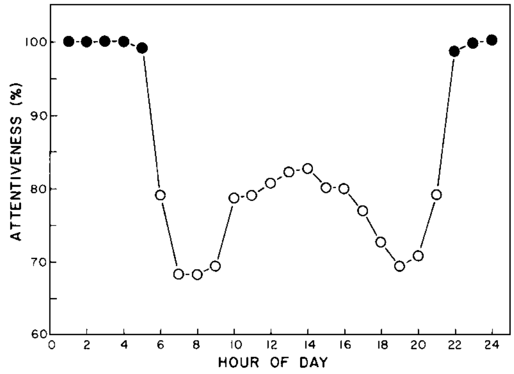

Fig. 6. Relationship of attentiveness to time of day in *Empidonax oberholseri.* Closed circles show data from hours of night rest, open circles from hours of active day. *n* is ca. 1,500 for each data point. Data were taken at 3-min intervals from 8 nests.

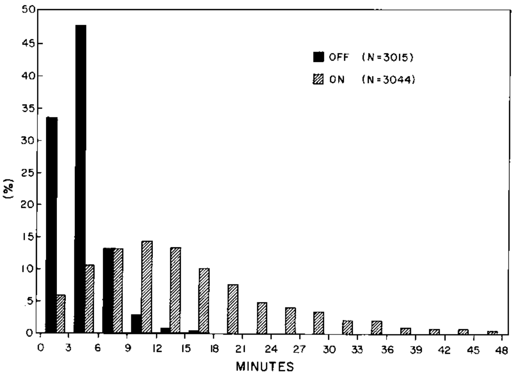

Fig. 8. Frequency (%) of bout durations in incubating *Empidonax oberholseri.* Bout classes encompassing fewer than 1% of cases are not shown.

egg-cooling, but it seems clear that she was not hypothermic at the time eggs were rewarmed. The reheating process began abruptly and proceeded at a rate of 1-2°C/min, which is typical of the records obtained when normothermic *E. oberholseri* came back onto cold eggs. Also, eggs were only 16.4°C and 21.7°C on 8 and 9 July when the female got off to feed. In contrast, when eggs are warmed during arousal from hypothermia by incubating hummingbirds, T_{egg} begins to increase gradually, the rate of increase is less than half that observed in *E. oberholseri,* and the female does not leave until T_{egg} (and her own T_b) are well above 30°C (Calder and Booser 1973, Vleck 1981b).

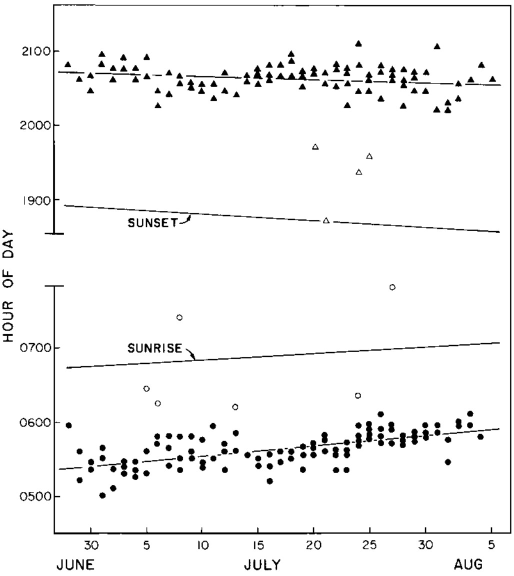

Fig. 7. Times of onset (bottom, circles) and cessation (top, triangles) of active day in *Empidonax oberholseri* throughout the nesting season. Data points shown as open symbols were associated with inclement weather (see text) and were not used in calculations of regression lines.

The data from nest 8 on 9 July (Fig. 5, bottom) are of additional interest in that they illustrate clearly the vagaries of summer weather at high altitude. Only a few hours after freezing T_as and high winds, the air became calm and was warmed rapidly by the sun. Eggs then became subject to solar heating, and in the early afternoon the female, now panting at times, had to be on the nest to prevent eggs from overheating.

There were 4 eggs in nest 8. The first 2 laid were implanted with thermocouples; the other 2 hatched and the nestlings fledged. Embryonic development probably was slowed by the spell of cold, windy weather because the incubation period (17 days) in this nest was longer than that usually observed by us in *E. oberholseri* (15 or 16 days) at Tioga Pass.

Attentiveness patterns during incubation.—Once full-time incubation began, and in the absence of foul weather, attentiveness in *E. oberholseri* had a predictable daily pattern. During the active day it tended to be below 70% early and late in the day and near or above 80% at midday (Fig. 6). The constancy of incubation (total time on the nest during the active day) for each of

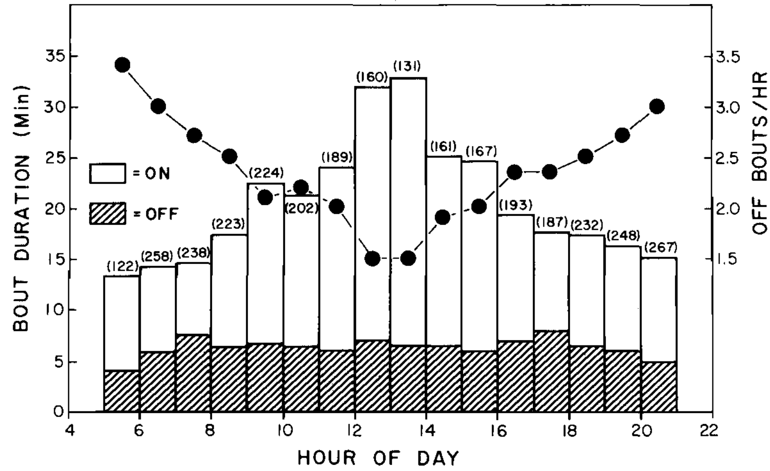

Fig. 9. Mean duration of on and off bouts (histograms, left ordinate) and mean frequency of off bouts (filled circles, right ordinate) with time of day in *Empidonax oberholseri*. Sample sizes are in parentheses.

5 nests for the full period of incubation was 75.1, 73.5, 72.0, 76.3, and 81.9% ($\bar{x} = 75.8\%$).

The active day began later as the season progressed (Fig. 7, bottom) and ended earlier (Fig. 7, top). Regression lines fitted to the data points by the least-squares method suggest that the trends were probably related to light intensity or photoperiod because they closely paralleled those describing sunrise and sunset. Total seasonal decrease in photoperiod during times of incubation was 40.2 min, whereas decrease in active day for the corresponding period was 42.6 min. Occasionally, females started their active day unusually late or ended it early. In every case the behavior was linked with inclement weather. Mean duration of active day was 891.1 min (SD = 59.2 min, range = 435–1,056 min, $n = 97$).

The durations of off (inattentive) and on (attentive) bouts during the active day were quite different in their frequency distributions (Fig. 8). Periods off tended to be brief; 82% were 6 min or less. Periods on were more widely distributed and were nearly 3 times longer in mean duration (19.3 min vs. 6.8 min).

During the active day, periods off changed by only a few minutes (Fig. 9). Attentive periods varied greatly, however, being 2–3 times longer at midday than in early morning and late evening. A corollary, of course, is that the rate of feeding trips changed. Their frequency was 3 or more/h at the onset and end of the active day but only 1.5/h at midday (Fig. 9).

The diurnal rhythm in constancy of incubation (Fig. 6) and in duration of on bouts leads one to ask if attentiveness changed with T_a. Attentiveness can shift during storms, but these occasions were relatively rare and the effects unpredictable in scope. During mild weather, however, there was a predictable relationship between attentiveness and T_a. The duration of on bouts, but not off bouts, increased as T_a increased (Fig. 10), and total attentiveness during

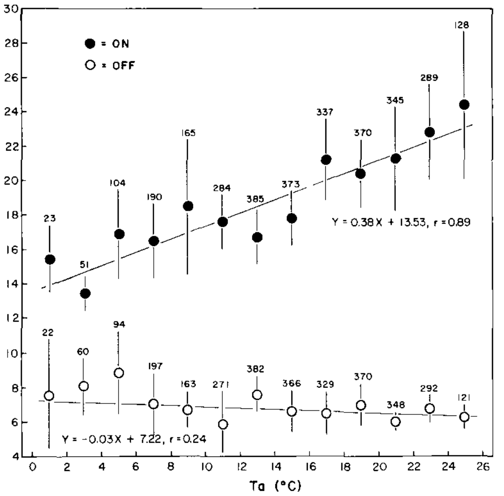

Fig. 10. Duration of on and off bouts with air temperature (T_a) in *Empidonax oberholseri*. Means ± 2 SE (vertical lines) are shown. Sample sizes are above each mean.

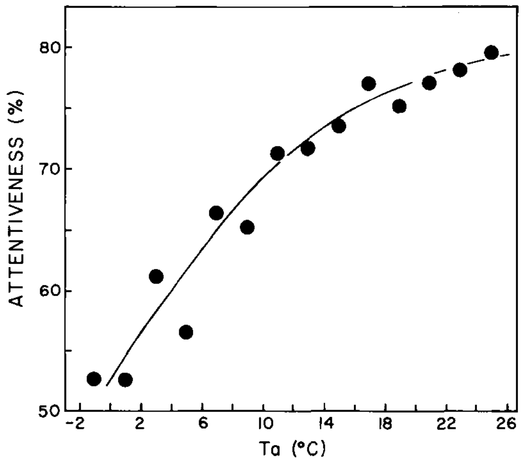

Fig. 11. Attentiveness (% time on nest during active day) vs. air temperature (T_a) in *Empidonax oberholseri*. Data are from 8 nests. Curved line was fitted by eye.

the active day increased steadily with T_a (Fig. 11).

Discussion

Attentiveness and temperature during the egg-laying period.—A striking aspect of attentiveness was that it consistently occurred during daylight hours prior to clutch completion. We suggest that this behavior is important because eggs were often exposed directly to solar radiation. Regular visits by the female would assure that such exposures would be too brief to be fatal. This is particularly true early in the season when vegetative canopies (leaves) may not yet be fully developed. *Empidonax oberholseri* embryos in the early stages of a clutch were sometimes maintained at temperatures permitting development (Fig. 1). However, if we accept 28°C as the minimum T_{egg} for embryo development (Drent 1975), we can see that this threshold value was actually exceeded only 17.6% of the time during the laying period (Table 3). A very similar daytime attentiveness pattern during laying was observed in *Z. l. oriantha,* another open-nester, on this same study area (Zerba and Morton 1983a).

Attentiveness at night prior to full clutch completion is not unusual. It seems to occur in all passerines that have been carefully studied and has been previously observed in several Empidonaces (King 1955, Davis et al. 1963, Mumford 1964). Haftorn (1978a) pointed out that this may protect embryos from low temperatures. However, eggs are routinely neglected in many species when it is cold, so the situation remains unclear. To our knowledge, only in the Black-tailed Godwit (*Limosa limosa,* Lind 1961) is there facultative nighttime sitting during the laying period in response to unusually cold weather.

Average T_{egg}/day was always 34°C or higher once full-time incubation began (Table 1), and T_{egg} was kept above the developmental threshold (28°C) 92.2% of the time during the active day and 99.9% of the time during night rest (Table 3). This seems remarkable given the frequency at which females foraged, especially because foraging trips occurred most often during the coldest parts of the active day. Maintenance of high mean T_{egg} was possible because females usually left the nest for short periods. Foraging trip duration was independent of T_a, and for more than 80% of the time was held to 6 min or less (Fig. 8). This meant that eggs usually cooled only slightly and could be restored quickly to high temperature upon resumption of incubation.

When females were exhibiting constant attentiveness, T_{egg} was 38°C or higher except during the first few days of incubation (Table 2). This last effect was probably due to changes in brood-patch function because full vascularization of the patch does not occur in many species until incubation is well underway (Drent 1975). Our measurements showing that brood-patch temperature increased as incubation progressed support this interpretation.

Because foraging trips by females coincided with the day's coldest air temperatures (Fig. 2), embryos experienced large and frequent fluctuations in temperature. Toleration of such oscillations, even when they are prolonged, might be a key adaptation of birds that breed at high altitude. It has been suggested, however, that excursions of this type usually are not a problem and might actually stimulate embryo development (Kendeigh 1940, Lundy 1969), thus compensating for the time that temperatures were below optimum levels.

The regular decrease in T_{egg} within the T_a range of 12–4°C during night rest (when females sit continuously) and the reversal of this trend at still colder T_as (Fig. 3) points to functionally significant changes in heat flow and heat generation. The total change in mean T_{egg} was 2.5°C; not a large effect but one that is statistically significant. If one accepts the view that the eggs and incubating parent function thermally as a unit (see Drent 1972, 1975), these data indicate that core T_b in females was labile. For a time T_b apparently decreased as T_a decreased. Warming of the bird and its eggs at still lower T_as (below 4°C) could occur only if females were shivering. This is similar to data obtained on *Z. l. oriantha* (Zerba and Morton 1983a) occupying aerial nests at Tioga Pass except that T_as sufficient to induce shivering in *Z. l. oriantha* were about 6°C higher than in *E. oberholseri*. Biebach (1979) found that increases in metabolic rate could be used effectively by European Starlings (*Sturnus vulgaris*) to maintain high T_{egg}s even at subfreezing T_as.

Ettinger and King (1980) found that daily energy expenditure of female *E. traillii* reached a minimum during the incubation phase of the breeding season. This matches well with our observation that incubating *E. oberholseri* had visible subdermal fat stores. These reserves must help to buffer the energetic consequences of cold weather and storms. Typically, summer storms on the study area were violent but brief (under 2 h). In many cases females could probably remain on their eggs and protect them for the storm's full duration. We are certain that eggs need protecting because females that leave the nest during hailstorms sometimes lose their eggs from breakage by hailstones (Pereyra and Morton MS).

We have not evaluated foraging efficiency in *E. oberholseri*. They are primarily sit-and-wait predators that fly out from perches to take prey. We have also observed them gleaning tree bark and foraging on the ground. Whatever their feeding techniques, they usually must be highly efficient. For example, several times we have seen females complete clutches during snowstorms that were severe enough to cause *Z. l. oriantha* to abandon nests entirely.

Skutch (1976) made the often-cited observation that birds hurry to their eggs and cover them when rain begins. He also observed that if the storm is prolonged, the parent will eventually leave to feed, and that in flycatching species foraging time may actually increase during storms because insects become hard to find. This response seems to have occurred during a heavy hail and rainstorm at nest 15 (Fig. 4). A similar pattern was also recorded during rainstorms in *R. regulus* (Haftorn 1978a, b).

During a series of cold and very windy days and nights, T_{egg} measurements in another nest of *E. oberholseri* (nest 8) indicated that toward the end of two successive periods of night rest, the female stopped applying her brood patch to the eggs (Fig. 5). This caused T_{egg} to decrease for a time to levels below those required for embryo development, but presumably it also assisted the female in her efforts to maintain normothermia.

Ordinarily, small birds seem able to produce enough heat at low T_as to maintain easily both T_{egg} and T_b (Biebach 1979, 1981; Vleck 1981a). At nest 8 continuous high winds coupled with low T_as probably reduced food availability and greatly increased heat loss from the bird-egg-nest complex. The incubating female, with insufficient energy reserves to fuel appropriate levels of shivering thermogenesis, was able to reduce heat loss from her body core by standing above the eggs instead of applying her patch to them. As pointed out by Drent (1975) for birds in hot environments, the parent's main problem while incubating is to maintain its own T_b in the face of environmental stresses. The same principle may apply to birds in the cold, particularly when energy reserves are depleted because of food scarcity.

Attentiveness.—Incubating females usually began their active day about 75 min before sunrise and ended it about 110 min after sunset. The pattern was seasonally consistent, indicating that it probably was cued by light intensity (Fig. 7). Major deviations did occur, however. The active day was sometimes shortened by as much as 2 h when it was very windy or a storm was in progress. Thus, females sometimes compensated for harsh environmental conditions by increasing their attentiveness.

The mean constancy of incubation in *E. oberholseri* was 75.8%. This is within the range of 60–80% reported by Skutch (1976) for numerous species and similar to that reported for congeners by Davis (1954), Davis et al. (1963), Mumford (1964), and Ettinger and King (1980). We have frequently observed incubating female *E. oberholseri* being fed by their mates both on and off the nest. The effect of this behavior on the female's time and energy budget and its ubiquity among Empidonaces are still open questions, but it could be contributing to an increase in attentiveness.

Foraging bouts by females usually were brief (Fig. 8), and there was little deviation in length of feeding trips with time of day (Fig. 9) or with T_a (Fig. 10), although the shortest trips tended to be the first and last ones of the active day (Fig. 11). A notable exception to this occurred before and after the first night of incubation, when off bouts were always very long (Fig. 1).

The frequency of foraging trips, on the other hand, varied diurnally. Off bouts averaged only 1.5/h at midday but occurred at twice that rate at the beginning and end of the active day (Fig. 9). This modification of foraging behavior was linked, naturally, to changes in duration of on bouts, which were longest at midday (Fig. 9). The result was a diurnal pattern wherein attentiveness was greatest from midmorning to midafternoon (Fig. 6).

The duration of on bouts correlated positively with T_a (Fig. 10). Given the constancy of off-bout duration, a strong positive relationship emerged between attentiveness and T_a (Fig. 11). This was unexpected. Usually, attentiveness decreases in passerines as T_a increases (see Drent 1972, 1975; White and Kinney 1974; Haftorn 1978a, 1979, 1981). Exceptions to this pattern have been found, however, and even predicted (Drent 1972). Desert birds may come back on at very high T_as and incubate constantly to prevent eggs from overheating (Maclean 1967, Russell 1969, Walsberg and Voss-Roberts 1983). Vleck (1981b) found that attentiveness was independent of T_a in Anna's (*Calypte anna*) and Black-chinned (*Archilochus alexandri*) hummingbirds or that it increased with T_a in Costa's Hummingbird (*C. costae*). Zerba and Morton (1983b) saw little change in attentiveness in *Z. l. oriantha* until T_a increased to 20°C; thereafter attentiveness increased rapidly. In *E. difficilis* attendance did not correlate with T_a, although the longest attentive periods observed (ca. 3 h) did occur on very hot days (Davis et al. 1963).

White and Kinney (1974) formulated a widely accepted model describing the relationship of attentiveness to T_a in single-sex intermittent incubators. They show that attentiveness decreased as T_a increased, eventually ceasing altogether when T_a equaled mean maximum T_{egg} (ca. 37°C). However valid the model of White and Kinney for the Village Weaver (*Ploceus cucullatus*) and other species that they considered, it is clearly inappropriate for the two species studied at high altitude (Fig. 12). At Tioga Pass both *Z. l. oriantha* (Zerba and Morton 1983b) and *E. oberholseri* (Fig. 10) lengthened their attentive bouts as T_a increased, exactly opposite to the response predicted by White and Kinney. We suggest that the attentiveness pattern of a species varies in accordance with selective pressures imposed by its environment. At Tioga Pass, T_a is always well below levels that would be troublesome to embryos. On the other hand, solar radiation can be intense, and eggs within a nest exposed to direct sun are rapidly heated to lethal temperatures (Zerba and Morton 1983b). Given the usual coincidence of high T_a and insolation, we conclude that *E. oberholseri* exhibits compensatory behavior in anticipation of potentially harmful environmental conditions. Such anticipation is particularly important because damage to eggs from overheating can occur quickly. It is also irreversible and must always be prevented in the first place (Drent 1975). We saw the anticipatory response (long on bouts at high T_as) in *E. oberholseri* during the laying period and even in cases where the nest was completely shielded from direct sun. Apparently the most appropriate behavior for females at high altitude is to stay on their nests as much as possible when it is hot. This would eliminate errors in evaluating moment-to-moment exposure of eggs to sun, a situation that can change quickly depending upon time of day and cloud cover. Also, nest exposure often changes greatly as foliage develops seasonally and when nests are relocated upon loss of a clutch.

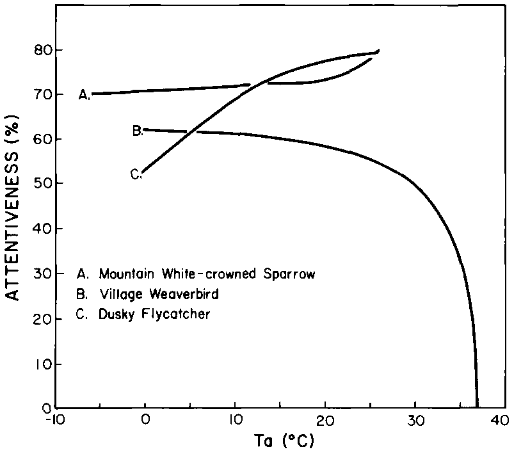

Fig. 12. Attentiveness (% time on nest during active day) vs. air temperature (T_a) in three species: Mountain White-crowned Sparrow (Zerba and Morton 1983b), Village Weaver (White and Kinney 1974), and Dusky Flycatcher (this study).

Additional benefits of long attentive bouts are that they diminish the energetic cost of incubation (Drent 1972, Vleck 1981a), promote faster embryonic development, and maximize the female's ability to protect eggs from predators (Drent 1972, 1975).

As pointed out by Carey (1980b), it is often difficult in cases of environmental adaptation to determine routes of natural selection or even which factor in the environment is the selecting agent. We propose that in *E. oberholseri* attentive behavior evolved in response to both food availability and dangers from solar heating of eggs. The most favorable pattern is for the bird to feed intensively during the early morning and late afternoon hours, when exposure to sun is least likely. This is feasible because they probably are highly adept foragers and because their embryos tolerate rapid cooling, low temperatures, and rapid reheating. The fact that this pattern of attentiveness is followed in both shaded and unshaded nests suggests that insolation is the selecting factor but that T_a is the environmental cue directing incubation behavior.

Temporary hypothermia of the incubating bird, egg neglect, and feeding of the incubating female by her mate have all been identified as adaptive reactions that could reduce the conflict between attentiveness and foraging time in small, single-sex incubators, thus allowing them to breed in cold regions (Walsberg and King 1978, Carey 1980a). The latter two of these responses, at least, have now been observed in *E. oberholseri*.

ACKNOWLEDGMENTS

We thank Eileen and Kim Zerba for assistance with computer programs. Ned K. Johnson and Carol M. Vleck kindly read the manuscript and made many helpful suggestions. Financial support was provided by Occidental College, California Foundation for Biochemical Research, National Science Foundation (Grant No. DEB 81-0651), and Mr. and Mrs. Alexander C. Ridland.

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The **1985 Raptor Research Foundation International Meeting and Symposium on the Management of Birds of Prey** will be held at the Capitol Plaza Holiday Inn in Sacramento, California, **2-20 November 1985**. For more information or if you are interested in presenting a paper, contact **Dr. Richard R. Olendorff, U.S. Bureau of Land Management, 2800 Cottage Way, Sacramento, California 95825,** or **Nancy Venizelos, San Francisco Zoological Society, Sloat Boulevard at the Pacific Ocean, San Francisco, California 94132.**

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The American Ornithologists' Union solicits nominations for its **Brewster and Coues Awards**. Nominations and supporting materials should be sent to **Dr. Abbot S. Gaunt, Department of Zoology, The Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210-1293.** Materials must be received before **1 June 1985.**

SOME EFFECTS OF WING TAGS ON BREEDING RING-BILLED GULLS

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ABSTRACT.—We examined the effects of wing tags on breeding Ring-billed Gulls (*Larus delawarensis*) by comparing the performance of tagged birds with that of color-banded birds. During the year of marking, effects seemed minimal. The following year, however, substantial differences were observed between the two groups. Fewer tagged birds returned to the colony and those that did were six days later, on average, than banded birds. About 60% of the tagged females were unable to acquire mates in the year after marking, but tagged males paired without apparent problems. Mean hatching date of tagged birds was three days later than banded birds. A large proportion of this group failed to raise any young, principally because tags seemed to interfere with pairing. Wing tags also may have affected birds at later stages of the reproductive cycle, but brood sizes for successful tagged and banded birds were similar in the year after marking. *Received 14 March 1984, accepted 9 June 1984.*

LONG-TERM studies of long-lived avian species often require that individuals be readily identifiable for a period of some years. In the last two decades, the patagial tag has been one of the more popular marking techniques used on birds (reviews in Marion and Shamis 1977, Kochert et al. 1983).

The use of plastic wing tags on Ring-billed Gulls (*Larus delawarensis*) was pioneered in 1967 at the Calcite colony in northern Michigan (Southern 1971). We continued to wing-mark gulls at this site intermittently through 1982. Many marked birds returned to the colony year after year; many apparently bred normally. On the basis of such casual observations, we considered the effects of tags to be negligible. Burley et al. (1982), however, recently found that color marking may have significant effects on bird behavior.

To evaluate the potential impact of tags on ring-bills, in 1982 we marked a second sample of birds with conspicuous color bands. Color-banded Ring-billed Gulls may not represent a true control group; however, we suggest that meaningful comparisons can be made between tagged and color-banded ring-bills to demonstrate some of the effects of tags. This paper summarizes our comparative observations on breeding performance of tagged and banded birds, primarily in the year after they were marked.

METHODS

Our study was conducted at the Calcite colony near Rogers City, Michigan (Presque Isle Co., 45°N, 83°W). On 19 and 24 May 1982, during the late incubation stage, we cannon-netted 279 nesting Ring-billed Gulls in study plots semipermanently marked with surveyor stakes. We wrapped a yellow, disc-shaped Saflag wing marker around the patagium of 150 birds, fastening the ends with an aluminum eyelet and 1 or 2 heavy-duty staples. We marked 53 other individuals with 1 or 2 Darvic color bands (J. E. Warner, Durham, England). Color bands were yellow, orange, white, black, blue, and green. All marked birds were in non-edge, traditionally used areas of the colony. Nests of color-banded birds were intermingled with those of some wing-marked birds. We have no reason to suspect that age structure or other potentially biasing factors differed between the banded and tagged samples.

In 1982 one of us (LKS) spent 163 h after cannon-netting observing newly marked birds from a car or truck that served as a blind. Between 6 April and 6 July 1983, LKS observed marked birds for 317 h, recording dates of first sighting and hatching and number of young reared to 21 days of age. When hatching was not observed firsthand, the date of hatching was determined by estimating the age of the oldest chick. The accuracy of this method was tested with known-age chicks unfamiliar to LKS, and 9 of the 10 estimates were within 1 day of the actual hatching date. None of the study plots was entered by any person once chicks were more than 2 days old.

TABLE 1. Rates of return of tagged and banded samples to the Rogers City colony site in 1983, and mean return dates in April.

	Tagged	Banded	*P*
Returning birds			
Number	92	48	0.0001[a]
Proportion	61.3%	90.6%	
Dates of return[b]			
All birds (122)	18.0 ± 11.4	12.0 ± 7.7	<0.001[c]
Females (73)	17.5 ± 9.2	10.7 ± 6.9	<0.001[c]
Males (45)	18.8 ± 14.7	12.2 ± 8.3	<0.05[c]

[a] χ^2 test.

[b] Numbers represent dates in the month of April.

[c] Mann-Whitney *U*-test.

TABLE 2. Breeding status of marked birds in 1983, the year following marking.

	Paired		Unpaired
Females			
Tagged	13 (37.1%)	**[a]	22 (62.9%)
Banded	24 (92.3%)		2 (7.7%)
Males			
Tagged	33 (94.3%)		2 (5.7%)
Banded	18 (100.0%)		0

[a] ** $\chi^2 = 16.78$, df = 1, $P < 0.0001$.

Rates of return to the colony site were determined by persistent searches for marked birds. Ring-bills at this colony show very strong nest-site fidelity, with between-year movements averaging about 1.1 m (pers. obs.), thus facilitating searches for marked individuals. Because of the probability that some tags had been lost, whenever possible we read band numbers of birds within the study plots. Three birds tagged in 1982 had lost their tags in 1983 but were identified by bands.

RESULTS

The year after they were color marked, 61.3% of the tagged sample and 90.6% of the color-banded sample were observed at the Calcite colony (Table 1).

Wing-tagged birds arrived at the colony site, on average, 6 days later than color-banded birds (Table 1). When categorized by sex, this difference still holds in the mean values. Because it appeared that tagged birds arrived later than banded birds, the alternate hypotheses for statistical testing indicated one-tailed tests were appropriate. The difference between the highly variable male samples was barely statistically significant, while females were highly significantly different (Table 1).

In the year of capture all tagged (35) and banded (11) males for which breeding status was determined were paired and held territories. For females for which breeding status was determined, 60 of 61 tagged birds were known to be paired, and all color-banded (18) birds were mated.

The year after marking, 37.1% of the tagged females that returned still wearing their tags acquired mates, while 92.3% of returning color-banded ones did so (Table 2). Of the 22 tagged females without mates, at least 13 (59.1%) were paired the previous year. In contrast to females, males successfully acquired mates in 1983 whether they were tagged or color-banded (Table 2). All but 1 of these males, a tagged individual, also held territories in the year after marking.

In 1983 greater proportions of banded birds reached egg, chick, and fledgling stages than did tagged birds. Almost all returning banded birds reached the egg stage (44 of 46 cases, 95.7%), whereas 62.9% of tagged birds did so (44 of 70 cases, $\chi^2 = 16.30$, df = 1, $P = 0.0001$). For birds that reached the egg stage, the chance of progressing through subsequent stages was similar for tagged and banded individuals ($\chi^2 = 1.05$, df = 2, $P = 0.59$).

Hatching dates were determined for the eggs of 31 tagged birds and 34 color-banded ones in the year after marking. On average, tagged birds hatched eggs 3 days later than banded birds ($t = 2.62$, df = 1, $P = 0.0056$).

Successful tagged and banded birds reared statistically similar numbers of young in both 1982 and 1983 (Table 3). If one considers reproductive success of all birds, i.e. including failures, 1982 mean brood sizes again did not differ for the two groups. The following year, however, each color-banded bird raised an average of 0.95 young and each tagged bird 0.36 young. The number of young fledged dropped significantly in the year after marking for tagged birds but showed no signficant difference for banded birds (Table 3).

The principal cause of reproductive failure for tagged females in 1983 was the inability to form pair bonds (Table 4). Some tagged males

TABLE 3. Mean brood sizes of marked birds. The category of "All birds" includes those known to have raised no young.

	1982	1983	
Successful birds			
Tagged (48)	1.45 ± 0.57	1.59 ± 0.71	$P(\chi^2) = 0.51$
Banded (39)	1.71 ± 0.73	1.56 ± 0.51	$P(\chi^2) = 0.14$
	$P(\chi^2) = 0.33$	$P(\chi^2) = 0.13$	
All birds			
Tagged (112)	1.22 ± 0.75	0.36 ± 0.75	$P(\chi^2) < 0.0001$
Banded (58)	1.41 ± 0.94	0.95 ± 0.87	$P(\chi^2) = 0.08$
	$P(\chi^2) = 0.53$	$P(\chi^2) = 0.0001$	

failed at each stage of the reproductive cycle (Table 4). All pairs with both members tagged laid and incubated eggs, but 8 later failed (Table 4); only 1 such pair fledged young. There were 5 pairs with both members color-banded, and all fledged young in the year after marking.

About one month after most birds had returned to the colony site (20 May 1983), we captured, weighed, and measured 22 tagged and 30 unmarked birds for which sex was known from behavioral observations. Birds with wing tags were not significantly different from unmarked birds in bill length and depth (Table 5). The 7 tagged females weighed slightly more, on average, than unmarked females, but the difference was not significant and may be due to slight differences in stages of the reproductive cycle. Tagged males averaged about 25 g less than unmarked males, a difference of borderline statistical significance ($t = 1.68$, df = 30, $P = 0.05$).

DISCUSSION

A significantly lower proportion of wing-marked Ring-billed Gulls returned to the colony site in the year after marking than did color-banded birds. Some tagged birds might have moved to other colony sites. However, in the many years we have tagged ring-bills, reports of these birds at other Great Lakes colonies have been extremely rare (3 in the last 5 yr, for example). A more likely explanation for the lower return rate of tagged birds is that the markers interfered with migration, as Howe (1980) proposed for Willets (*Catoptrophorus semipalmatus*). This explanation is supported by the fact that tagged birds returned to the Rogers City site about 6 days later than color-banded birds.

Tagged males were able to acquire territories and mates as readily as color-banded males. About 60% of the tagged females did not pair in the year after they were marked, although not for lack of trying. Many of these females approached and solicited males even after the time chicks had hatched. For years we have noticed the presence of outcast tagged females, and we now consider this to be caused by the markers.

In the year of marking no obvious differences were noted in breeding performance of tagged and banded birds. In an earlier study, however, we observed slightly lower brood sizes during the year of marking for successful, tagged gulls as compared to successful, un-

TABLE 4. Stage of reproductive failure in 1983 for birds marked in 1982. Unless otherwise noted, birds had mates that were unmarked or carried only an aluminum band. Only those failures whose mates and status were known at all stages are included.

	Stage of failure[a]			
	Pairing	Egg-laying	Hatching	Fledging
Tagged ♀♀	22	0	1	0
Banded ♀♀	2	0	2	0
Tagged ♂♂	2	2	4	2
Banded ♂♂	0	0	3	1
Tagged ♀♀ with tagged ♂♂	—	0	5	3
Banded ♀♀ with tagged ♂♂	—	0	0	3

[a] Pairing = failed to form pair bond; egg-laying = paired, but no eggs laid; hatching = eggs lost or not hatched; fledging = chicks died before 21 days old.

TABLE 5. Bill measurements and weights of tagged and unmarked birds captured on 20 May 1983. In this case, tagged birds were ones that had carried markers for 1-5 yr.

	Bill length (mm)	Bill depth (mm)	Weight (g)
Females			
Tagged (7)	55.1 ± 3.4	12.6 ± 1.0	480.7 ± 49.3
Unmarked (13)	55.8 ± 2.3	12.7 ± 0.7	476.5 ± 27.3
P(t)	0.50	0.49	0.40
Males			
Tagged (15)	60.9 ± 2.6	13.9 ± 0.7	525.0 ± 48.6
Unmarked (17)	61.4 ± 2.1	14.2 ± 0.7	550.9 ± 38.6
P(t)	0.28	0.14	0.05

marked birds (Southern and Southern 1983). Sample sizes were larger in that study, and the potential for immediate impacts on reproduction must be acknowledged.

In the year following marking, 61.0% of banded birds and 25.4% of tagged birds raised young ($\chi^2 = 13.56$, df = 1, $P = 0.0002$). Brood sizes were similar for successful tagged and banded birds. However, a large proportion of tagged birds failed to breed at all, principally because tags seemed to interfere with pair bonding. The delayed arrival of tagged females may have contributed to their difficulty in establishing pair bonds, but it probably was not the most important factor. Some very early females failed to pair, while some lates ones succeeded. There also were indications that tags affected birds at later stages of the reproductive cycle. Eight of 9 tagged pairs (88.9%), for example, failed to raise young, while 100% of 5 banded pairs succeeded. At least 7, and possibly all 9, of the tagged pairs had been mated to each other the previous year. Although their pair bonds were maintained following marking, their reproductive success was extremely low.

Taking into account the weight of a tag and band, tagged males weighed about 4% less than unmarked males. Impacts of tags on flight or foraging efficiency would not be surprising, but this possibility remains to be investigated.

In most studies of wing-marked birds, investigators have assumed that if *some* tagged birds appeared to behave normally, then any marker effect must be negligible (e.g. Hewitt and Austin-Smith 1966, Rowley and Saunders 1980). Only a comparison of the sort discussed in this paper, however, can accurately determine whether or not tags have a detrimental effect. In addition, some impacts of tags will be observed only during long-term studies, and other effects may be noticeable primarily in the nonbreeding season.

As others have suggested previously (e.g. Kochert et al. 1983), marking techniques must be tailored to the species and should be carefully evaluated whenever possible. This is particularly important for sensitive and rare species; in our view, patagial tags should be used on such forms only with the utmost caution. For other species or for some purposes, patagial markers may be the only viable alternative. To ensure accurate representation of natural phenomena, we urge further scrutiny of the effects of color marking.

ACKNOWLEDGMENTS

We thank T. Dudek, L. Hansen, K. Hunt, G. Lutfy, N. Lutfy, J. Mellen, and M. Southern for invaluable cannon-netting assistance. J. W. Fitzpatrick, D. E. Miller, and an anonymous reviewer provided helpful comments on the manuscript. C. F. Thompson encouraged this research, which was funded in part by a Grant-in-Aid of Research from Sigma Xi. The U.S. Steel Corp. granted us access to the colony site, and A. White kindly typed the manuscript.

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Birding With a Purpose

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by Frances Hamerstrom

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NUTRIENT CONTENT OF EGGS AND THE ENERGETICS OF CLUTCH FORMATION IN THE BOAT-TAILED GRACKLE

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ABSTRACT.—Shell, yolk, and albumen represent 10.5%, 21.9%, and 67.6%, respectively, of fresh-egg weight of Boat-tailed Grackles (*Quiscalus major*). The proportion of egg composed of dry yolk increases as egg weight increases. The average 8.1-g egg contains 33.6 kJ of which 66.1% is in yolk and 33.9% is in albumen. The average three-egg clutch was estimated to cost 131 kJ for yolk development and albumen deposition. These costs were spread over a 6-day period, with a peak of 28 kJ occurring on the day before egg laying began. At hatching, the yolk sac represents 19% of hatchling wet weight. Only 10% of the energy present in the egg at laying is expended during incubation. Hatchlings have substantial yolk reserves that contain 49% of the hatchlings' energy. *Received 12 May 1983, accepted 9 June 1984.*

EGG size may vary greatly within populations and within clutches. The proportion of egg made up by yolk, albumen, and shell may vary with egg size (Ricklefs 1977a, 1984; Howe 1978; Nisbet 1978; Ricklefs et al. 1978; Ricklefs and Montevecchi 1979) and indicates variation in the energy females commit to clutch completion. The total energetic costs of egg formation include the energy required for ova development, growth of a functioning oviduct, albumen deposition, and shell deposition (King 1973, Ricklefs 1974). Few estimates are available for the energetic costs of clutch completion in altricial birds. The present paper analyzes the pattern of variation in the composition of eggs, energetic costs of clutch completion, and use of energy in the egg during incubation in the Boat-tailed Grackle (*Quiscalus major*).

METHODS

I collected eggs in March and April of 1980 and 1981 in Hillsborough Co., Florida. I collected seven clutches of three eggs on the day the third egg was laid and two single eggs on the morning they were laid. I collected one three-egg clutch when the first egg was pipped. Two eggs had been incubated for 12 days and one egg for 11 days. All eggs were weighed to the nearest 0.001 g and frozen for later analyses. Fresh eggs were separated into shell, egg white, and yolk. Eggs that were about to hatch were separated into embryo, yolk sac, and shell. Components were weighed and dried over concentrated sulfuric acid under a vacuum at room temperature. Dry weight was recorded and water content determined by subtraction. Total lipid content was determined by the chloroform-methanol extraction method of Freeman et al. (1957). Protein level was determined by the colorimetric method of Lowry et al. (1951), using bovine serum albumen as the standard. Ash content was determined by heating samples for 4 h at 500°C. Constants given by Brody (1945) and Kleiber (1961) were used to convert the g organic material into caloric units: 39.6 kJ/g lipid and 23.7 kJ/g protein.

Using Ricklefs's (1974) model, I estimated the costs of clutch formation from dry weight and energy content of yolk and albumen, rate of ovum growth, laying interval, and clutch size. No information was available on costs of oviduct development, costs of shell deposition, or modification of behavior, and they are not included in my estimates. Ricklefs (1976) found that the ova of European Starlings (*Sturnus vulgaris*) develop over a three-day period. I assumed that Boat-tailed Grackles have a similar pattern of ova development and calculated from his model that 58%, 23%, and 17% of the dry weight of each ovum was deposited on successive days of development. Each ovum in the clutch was assumed to begin development on successive days. Grackles typically lay one egg per morning until the clutch is complete (Bancroft 1983); therefore, the albumen for a given egg must be deposited in less than 24 h. Daily energy costs were calculated by multiplying the energy density by the weight of yolk or albumen deposited and assuming the costs of biosynthesis were 75% (see Ricklefs 1974). The cost curves were calculated based on the mean clutch weight of 24.2 g (Bancroft 1984a).

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TABLE 1. Weights (g) and composition (% of wet or dry weight or energy content) of Boat-tailed Grackle eggs in central Florida.

	n	Mean	SE	Minimum	Maximum
Total weight	23	7.72	0.13	6.59	8.90
Shell weight	23	0.81	0.02	0.61	0.97
Yolk weight	23	1.69	0.06	1.18	2.45
Albumen weight	23	5.22	0.09	4.48	6.02
Yolk					
Water (% wet weight)	23	60.5	0.9	55.0	71.1
Lipid (% dry weight)	22	56.3	0.6	51.3	61.9
Protein (% dry weight)	23	38.5	0.4	35.6	41.7
Ash (% dry weight)	20	2.6	0.2	1.4	4.7
Total energy (kJ)	22	20.70	0.6	15.69	27.43
Albumen					
Water (% wet weight)	23	90.7	0.1	89.3	91.9
Protein (% dry weight)	19	91.8	0.9	82.5	97.2
Ash (% dry weight)	19	5.7	0.2	3.7	7.1
Total energy (kJ)	19	10.62	0.20	8.98	11.87
Shell					
Water (% wet weight)	23	34.5	1.0	27.7	48.5
Yolk/albumen (dry)	23	1.37	0.03	0.99	1.62
Whole egg					
Water (% wet weight)	23	78.4	0.1	77.4	79.4
Energy (kJ/egg)	18	31.54	0.91	25.86	39.14
Energy (kJ/g wet weight)	18	4.06	0.05	3.69	4.40

RESULTS

Composition of eggs.—Table 1 presents the wet weight, dry weight, and composition of 23 Boat-tailed Grackle eggs that were collected within 2 days of laying. The percentage of water in the yolk varies (CV = 6.8%) more than that of the albumen (CV = 0.7%). Of the dry weight of egg contents, lipids represented 32.4% (SE = 0.1, $n = 22$). In composition, grackle eggs closely resemble those of other altricial birds (Ricklefs 1977b, Carey et al. 1980).

Between-clutch variation accounted for more than 55% of the variation in weight of egg components (Table 2). Significant variation with sequence of laying occurred only for yolk wet weight. Within-clutch variation in yolk wet weight accounted for 35.3% of the total variation, whereas for yolk dry weight within-clutch variation was only 12.6% of the total variation.

Because eggs showed strong within-clutch resemblances, I calculated correlation coefficients and regression equations based on clutch means. Fresh-egg weight was significantly correlated ($P < 0.05$) with water content ($r = 0.999$), wet and dry weights of yolk ($r = 0.829$, $r = 0.957$) and albumen ($r = 0.947$, $r = 0.751$), and dry weight of shell ($r = 0.912$), but not shell wet weight ($r = 0.600$, $P = 0.09$). Figure 1 shows the relationship between dry weight of yolk and fresh-egg weight. The slope of the functional regression (see Ricker 1973) was significantly greater than 1 ($t = 3.19$, $P < 0.05$). Energy content (EC) of the eggs showed a similar relationship to fresh-egg weight [$EC = 1.832\ wt^{1.391}$, $n = 9$, coefficient of determination (R^2) = 0.901, $P < 0.01$], but the slope for this equation was not quite significantly greater than 1 ($t = 2.36$, $P = 0.051$).

Temporal sequence of energy expenditure.—Energy-expenditure curves were calculated only for costs of ova development and albumen deposition (Fig. 2). The daily energy expenditure for ova development was highest on the day of first ovulation (Fig. 2). At this point all three ova were developing. Daily energy expenditure for egg development began as 17 kJ on the first day of ova development and reached a maximum (28 kJ) on the last day before laying began. Energy requirements decreased during laying because fewer eggs were developing. To produce the average clutch (24.2 g) a female needed 131 kJ over a six-day period. Half of all three-egg clutches weighed between 22.8 g and 25.5 g (Bancroft 1984a). Thus, energy expendi-

TABLE 2. The percentage of total variance in component weight attributable to differences within and between clutches of Boat-tailed Grackles.[a]

Component	Weight	Percent between clutch	Percent within clutch		
			Sequence[b]	Other[c]	F[d]
Wet yolk	1.68	64.7	22.7	12.6	10.36**
Wet albumen	5.16	57.0	8.6	34.5	2.85*
Water	6.00	68.5	11.3	20.1	5.95**
Dry yolk	0.65	87.3	4.5	8.1	16.92**
Dry albumen	0.48	66.4	9.5	24.1	4.73**

[a] Based on a two-way analysis of variance.

[b] Percentage of variance factored out by sequence of laying.

[c] Percentage of variance represented by error component.

[d] F = model mean square divided by error mean square; * $P < 0.05$; ** $P < 0.01$.

ture for half the population would have been between 123 and 139 kJ. The average clutch of two eggs weighed 16.3 g and needed 89 kJ to produce. Half of all two-egg clutches ranged from 15.1 to 17.3 g and required 82–94 kJ to produce.

From the equation of Kendeigh et al. (1977), I estimated a basal metabolic rate (BMR) of 89 kJ/day for female Boat-tailed Grackles. Energy requirements for laying were approximately 19% of BMR three days before laying, 31% of BMR on the day before the first egg was laid, and 16% of BMR on the day albumen for the last egg was synthesized (Fig. 2).

Energy content of hatchlings.—Just prior to hatching, yolk sacs in three eggs averaged 19% of wet and 45% of dry egg contents. The three eggs contained 28.4 kJ, compared to an estimated energy content of 31.7 kJ when laid. The remaining yolk contained 49% (14.0 kJ) of the energy. Of the energy estimated to be present in the yolk at laying (20.6 kJ), 68% was still present in the yolk sac just before hatching.

For Boat-tailed Grackles the lipid index of eggs (lipid weight/lipid-free dry weight of egg contents) averaged 0.482 (SE = 0.011, n = 22). The lipid index of two eggs that had been incubated 12 days averaged 0.362 with and 0.164 without the yolk sac. These two eggs were estimated to have lipid indices of 0.499 at laying.

DISCUSSION

Eggs of Boat-tailed Grackles averaged 8.1 g (n = 1,094) and ranged from 5.5 to 11.2 g (Bancroft 1984a). More than 80% of the variation in egg weight was attributable to between-clutch variation in weight. Egg weight varied significantly with laying sequence. Last-laid eggs in clutches of two and three were significantly lighter than earlier eggs. Although yolk wet weights of third eggs were less than those of the first two, dry weights showed no significant differences with laying sequence. This suggests that the average difference of 0.32 g (n = 161; Bancroft 1984a) between the weights of the first and last eggs in three-egg clutches results from differences in water content. The correlation between fresh-egg weight and organic content, and the significant between-clutch variation in wet and dry weight of components, clearly show that between-clutch variation is partly a result of differences in organic content. Organic content of eggs of Common Terns (*Sterna hirundo,* Nisbet 1978) and Common Grackles (*Quiscalus quiscula,* Howe 1978) did vary significantly with laying sequence as well as between clutches.

In Boat-tailed Grackles, yolk dry weight increased in direct proportion to fresh-egg weight. A similar pattern occurs in Common Grackles (Howe 1978); mean yolk content/clutch was directly correlated with mean dry weight, but albumen weight showed no significant correlation with egg dry weight. In the Starling, yolk size decreased in proportion to fresh-egg weight (Ricklefs 1977a, 1984). In the Northern Gannet (*Sula bassanus*), yolk size is independent of fresh-egg weight, whereas albumen size is directly correlated (Ricklefs and Montevecchi 1979). In the Common Tern and the Laughing Gull (*Larus atricilla*) the proportion of the egg composed of yolk decreased and albumen increased with an increase in egg weight (Nisbet 1978, Ricklefs et al. 1978).

The yolk/albumen ratio averaged 1.37 for Boat-tailed and 0.95 for Common grackles (Howe 1978). The mean dry weight of albumen

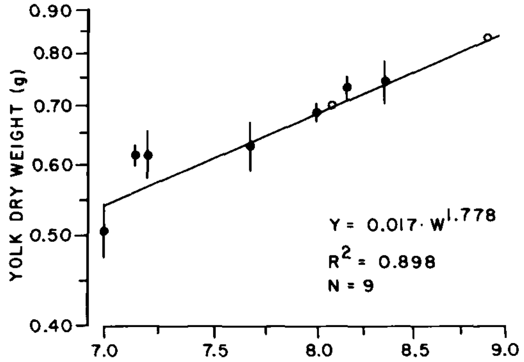

Fig. 1. Dry-yolk weight relative to fresh-egg weight of Boat-tailed Grackles in central Florida. Closed circles represent mean yolk and egg weight within 7 three-egg clutches. Vertical lines show one standard deviation on either side of mean. Open circles are for two single eggs.

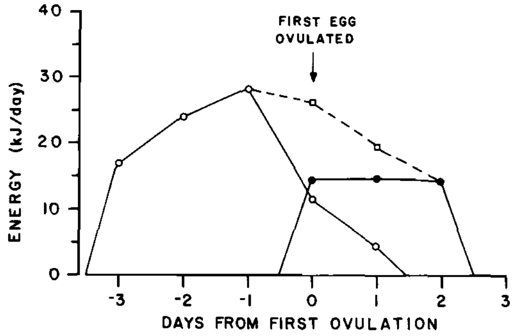

Fig. 2. Calculated mean daily energetic costs of yolk and albumen production in the Boat-tailed Grackle for a clutch of three eggs. Open circles represent daily costs of yolk production, closed circles represent daily costs of albumen production, and squares represent daily costs of yolk and albumen production combined.

for Boat-tailed and Common grackles was essentially equal. Thus, the difference in yolk/albumen ratio reflects the increased yolk size of Boat-tailed Grackles. Female Boat-tailed and Common grackles are similar in size, but Boat-tailed Grackle eggs average 1.2 g heavier (Howe 1978, Bancroft 1984a). Female nestlings of both species grow at close to the same rate and attain about the same weights at fledging, whereas male Boat-tailed Grackles fledge at 30–40 g heavier than Common Grackle males in about the same amount of time (Howe 1976, 1978, 1979; Bancroft 1983, 1984b).

The difference in yolk size between these two grackles may reflect a trade-off between number and size of eggs. Boat-tailed Grackles in Florida lay either two or three eggs, and the female raises the nestlings by herself (Bancroft 1983). Monogamous Common Grackles typically lay four or five eggs (Howe 1976, 1978), and the male helps care for nestlings (Howe 1979). Early in the nestling period Boat-tailed Grackle females must divide their time between brooding young and foraging. The young may need a larger yolk reserve for this period. In Common Grackles the male will provide some food during this period.

For Boat-tailed Grackles the total energetic cost of development while in the egg is relatively low. Eggs at hatching contained only 3.3 kJ (10.4%) less than when they were laid. Vleck et al. (1980) derived an equation for altricial birds that predicts the energy (*E*) used during incubation as a function of fresh-egg weight ($E = 0.59\ wt_{egg}^{0.78}$). This equation predicted that Boat-tailed Grackles should have expended 12.4 kJ of energy during incubation. Apparently, development is more costly in Red-winged Blackbirds (*Agelaius phoeniceus*) because blackbird hatchlings contained only 49% of the energy in freshly laid eggs (Fiala and Congdon 1983). The relatively low amount of energy used during incubation of grackle eggs was correlated with the large yolk sac remaining at hatching. The yolk sac of grackles represented 19% of hatchling weight. For 31 altricial species the yolk sac averaged 8% of wet weight at hatching (Romanoff 1944, Schmekel 1960, Vleck et al. 1980). For grackles the yolk sac contains sufficient nutrients and energy to sustain growth and maintenance through the day of hatching and into the next day (Bancroft 1983). Young usually are fed during this period, and the yolk reserve may last longer.

There may be a selective advantage in having larger yolk reserves at hatching. Yolk reserves provide nutrients necessary for growth during the first few days of the nestling period, when the female must divide her time between brooding and foraging. Hatchling weight was significantly correlated with fresh-egg weight (Bancroft 1984a), and future studies may show that larger eggs with proportionately more yolk provide hatchlings with greater yolk reserves. However, survival of third-hatched young through day 6 of the nestling period was not related to egg weight (Bancroft 1984a). Egg size influences growth rates of young in several species (Schifferli 1973, O'Connor 1975, Howe 1976), possibly including Boat-tailed Grackles. Grackles that attain asymptotic weights more quickly often will fledge earlier, and this may increase their chances of survival (Bancroft 1983, 1984b).

Female Great-tailed (*Quiscalus mexicanus*), Common, and Boat-tailed grackles have similar body weights and egg sizes (Selander and Giller 1961, Howe 1978, Bancroft 1984a). Because Great-tailed and Common grackles have larger clutch sizes, they expend more energy on clutch completion than do Boat-tailed Grackles. Peak daily energy requirements for egg formation of Boat-tailed Grackles was 31% of BMR, which was less than the 45% of the average BMR estimated for passerines (Ricklefs 1974). As a percentage of body weight, clutch weights of Boat-tailed Grackles also average less than some small passerines (King 1973, Ricklefs 1974, Rahn et al. 1975). This suggests that for Boat-tailed Grackles the relative energetic investment in a clutch is substantially below that of many passerines. Boat-tailed Grackles begin nesting in March (Bancroft 1983). Eggs laid during March are smaller (Bancroft 1984a) and presumably have proportionately less yolk than those laid later. Although Boat-tailed Grackles have a relatively low energetic commitment to egg production compared to other species (King 1973, Ricklefs 1974, Rahn et al. 1975), the smaller eggs during March suggest that grackles begin nesting before they can accumulate sufficient nutrients and energy to lay the largest egg possible.

ACKNOWLEDGMENTS

Glen E. Woolfenden provided the intellectual environment to undertake this study and the advice necessary to complete it. Field work was supported by grants from the Frank M. Chapman Memorial Fund of the American Museum of Natural History and from the Ding Darling Foundation. John M. Lawrence taught me the techniques for nutrient analysis and allowed me to use the equipment in his lab. Discussions with William Bros, Wayne Hoffman, John M. Lawrence, and Earl D. McCoy improved various aspects of this study. John M. Lawrence and Glen E. Woolfenden read and improved an early draft of the manuscript. Finally, I thank my wife, Ann, who provided help with field and laboratory work, and most of all provided invaluable encouragement and support throughout this project.

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CLUTCH SIZE, TIMING OF LAYING, AND REPRODUCTIVE SUCCESS IN A COLONY OF GREAT BLUE HERONS AND GREAT EGRETS

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ABSTRACT.—During a 13-yr period mean Great Blue Heron (*Ardea herodias*) clutch size at a central California colony ranged between 2.72 and 3.35 eggs, with an overall mean of 3.16. Mean Great Egret (*Casmerodius albus*) clutch size ranged from 2.70 to 3.07 eggs, with an overall mean of 2.87. Annual differences in clutch size were weakly significant in both species, and clutch size in both species declined slightly with relative as well as absolute time of breeding. The overall mean number of fledglings produced from heron nests was 1.45, with annual means ranging from 0.89 to 2.38. Year, clutch size, and relative time of breeding had significant effects on heron fledging success. The mean number of fledged egrets/nest was 0.90, ranging from 0.03 to 2.04 annually; only annual differences accounted for a significant proportion of the variance in fledging success. In both species, the most frequent clutch size was 3 but the most productive size was 4. Overall, 46.8% of the heron eggs and 33.0% of the egret eggs fledged young. The herons nested in smaller numbers and earlier than the egrets. Annual variability in colony mean clutch-initiation dates was less for herons than for the egrets. Egret clutch and brood sizes were smaller before the 1972 ban on DDT and related chemicals than after. Laying dates before and after the ban did not differ significantly. A similar comparison for the herons showed no significant differences associated with the ban on DDT. The herons lost more young to starvation than to predation, and the egrets displayed the opposite trend. Mortality of the young was greatest for the herons in the second week of life and greatest for the egrets in the third; survival for both species was high after 5 weeks. Except for a drop in the number of breeding pairs of egrets after a year of heavy predation, fluctuations in population levels were not correlated with reproductive biology. *Received 9 December 1983, accepted 7 July 1984.*

CONSIDERABLE attention has been focused on the reproductive success of the Ardeidae in the wake of the discovery that certain species are vulnerable to pesticide-induced eggshell thinning and egg loss during incubation (Vermeer and Reynolds 1970; Faber et al. 1972; Pratt 1972a; Ohlendorf et al. 1978, 1979; Blus et al. 1980; Findholt 1981; Mitchell 1981; Bayer 1982; LaPorte 1982; Custer et al. 1983a, b). However, the relative importance of ecological factors fundamental to productivity and abundance is poorly understood. Long-term studies are particularly valuable in this regard. Most recent studies of these species are of 1-3 years' duration and thus are limited in their potential for evaluating environmental determinants. Because short-term effects may vary from year to year, long-term trends would become apparent only after long periods of time, and rare but important events may be missed (Wiens 1984).

In this paper we analyze the relationships among clutch size, time of laying, and fledging success, and we evaluate the relative importance of starvation and predation on fledging success in a Great Blue Heron (*Ardea herodias*) and Great Egret (*Casmerodius albus*) colony in central California for the 13-yr period from 1967 through 1979. This paper differs from other heron and egret studies in two respects. It is the first long-term study of the Ardeidae that includes details on the breeding biologies of the species. It is also apparently the only study of the group that has been able to follow the

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breeding biologies of the birds in such detail without observer disturbance. The picture of breeding biology so obtained probably is closer to the natural situation than those obtained at colonies subject to observer disturbance. Nesting success at this colony for 1967–1973 has been reported previously (Pratt 1970, 1972a, b, 1974).

Heron and egret clutch size has been shown to vary with laying date (Jenni 1969, Wolford and Boag 1971, Siegfried 1972, Rodgers 1980a, Custer et al. 1983a). It may differ between years (Wolford and Boag 1971, Custer et al. 1983a) or it may remain constant (Rodgers 1980a, Tremblay and Ellison 1980, Custer et al. 1983a), and mean clutch size sometimes shows intercolony differences in similar habitats (Custer and Osborn 1977). Larger clutches usually produce more young (Tomlinson 1975; Rodgers 1980a, b; Tremblay and Ellison 1980) although St.Clair Raye and Burger (1979) found no significant differences in survival by clutch size for Snowy Egrets (*Egretta thula*) in New York, and results of studies by Millstein et al. (1970) and Morrison and Shanley (1978) are inconclusive.

STUDY AREA AND METHODS

Our data were gathered at the Audubon Canyon Ranch heronry on the central California coast (37°56′N, 122°41′W), where Great Blue Herons and Great Egrets nest in the same colony. The birds nest in or near the tops of 24–30 m tall coast redwoods (*Sequoia sempervirens*) that grow from the bottom and north-facing slope of a narrow canyon. The colony is roughly linear with no well-defined center (Fig. 1). It is known to have been active since 1941 and probably was established well before that time. It is 21 km from the nearest Great Blue Heron colony and 19 km from the nearest Great Egret colony.

Observers watched nests from an overlook approximately 11 × 5 m on the south-facing slope of the canyon above the level of many nests and about 90–180 m from them. This overlook has been heavily used by visiting school groups during the week and by the general public during weekends since 1962, when local Audubon societies purchased the ranch. We believe our results are not biased by investigator disturbance because the birds show no sign of alarm when humans are at the overlook, in part perhaps because of the distance to the nests and in part because the trail up the side of the canyon is concealed by trees and shrubs. The potential for disturbance is limited to the area of the overlook, where observers are quiet and movement is restricted.

Clutch and brood size were determined by looking into openly visible nests. Where nest placement or intervening foliage prevented accurate egg and chick counts, laying and hatching dates could be established to within 3 days by egg color, chick movement, and behavior of adults. Nest construction for both species is conspicuous, and several days elapse from the beginning of nest-building to clutch initiation. All nests were discovered in the building stage except for 5 or fewer egret nests/year that were built at hidden sites where activity of the adults or, if successful, large young revealed the location. In such cases the timing of nest events could only be inferred.

All nests were plotted and numbered on a diagram of the heronry as they were established, and their progress was followed until the last young left the colony. Observers checked nests using 7× binoculars and 20× spotting scopes at 3- or 4-day intervals, except in 1971 when checks were at 2- or 3-day intervals. On the night of 20 June 1975, when the colony was being devastated by nocturnal predation, observers kept watch from 2030 to 0020 to identify the predator.

The number of breeding pairs was defined as the maximum number of simultaneously occupied nests. Maximum heron nest occupancy occurred before any nests failed, and the number of nest starts after that date was always fewer than the number of early failures. Some egret nests failed before the time of maximum occupancy, especially during the years when thinned-shelled eggs were breaking in the nests, but nest initiations after maximum occupancy did not exceed early failures. We assume that nests built after maximum occupancy were initiated by pairs that failed earlier at Audubon Canyon Ranch, but because none of the birds was marked, we cannot exclude the possibility that birds that failed at other colonies came to Audubon Canyon Ranch to renest.

We considered young successfully fledged when they were old enough to fly across open space to trees away from the nests. This was 7 weeks of age for the egrets (Tomlinson 1976, Pratt MS) and 8 weeks for the herons (Vermeer 1969, Pratt 1970). Because observers did not disturb the young and because young hurried back to the nests when adults arrived to feed, it was possible to associate chicks with single nests until they were able to fly.

Young that died in nests with healthy siblings and young that disappeared sequentially in broods of 2–4 were considered to have died of starvation. Young categorized as lost to predators included losses in nests where there were bloody remains, losses where chicks were found on the ground with evidence of predator attack, and simultaneous losses where the whole brood vanished with no trace.

In our analyses of the effect of the timing on breeding biology, we used two measures of timing: 1) the absolute date of breeding, which corresponds to the calendar date of laying of the first egg, and 2) the

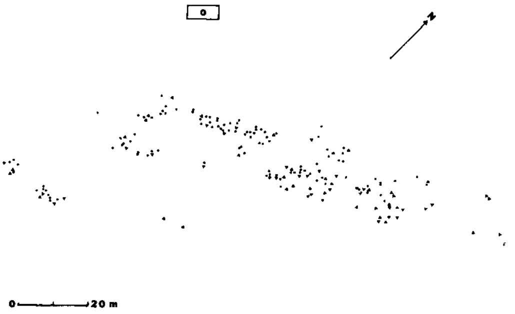

Fig. 1. Nest chart at Audubon Canyon Ranch for a representative year (1973). Triangles = heron nests, circles = egret nests, O = overlook.

"percent-ranked date of egg-laying," which is an index of the relative time of breeding within seasons with differing annual means of laying dates. The latter measure was computed by ranking the dates of nest initiations within each nesting season, dividing by the total number of nests in that season, and multiplying by 100. Thus, a percent-ranked date of breeding of 25 would apply to the third bird to lay in a group of 12, the 40th bird in a group of 160, and the 65th bird in a group of 260.

Statistical analyses were conducted with the Statistical Analysis System (SAS) operating on the University of California at Berkeley's IBM 4341 computer. We used SAS to run *t*-tests using the TTEST procedure, analyses of covariance (ANCOVA's) using the General Linear Models (GLM) procedure, and linear regressions using the SYSREG procedure. The ANCOVA is a statistical analysis similar to the analysis of variance. In the ANCOVA, however, the contribution of each of the various independent variables to the overall variance in the dependent variable is first factored out, if necessary, with linear regression. If, for example, one were to analyze differences in clutch size between years, but clutch size was known to decrease linearly with the time of laying, the most powerful statistical test for the effect of differences in years would be to first adjust for the fact that clutch size differs with time of laying. The ANCOVA's performed by SAS conduct such analyses, and they control for all other variables in the independent variable list when a given independent variable's effect is being tested. A further complication arises when the type of dependence (e.g. positive steep, negative shallow) of the dependent variable on the independent variable depends on the value of another independent variable. Such complications are termed "interaction effects," and in our analyses we tested for all such effects as well as the main effect of each independent variable taken alone. In interpreting ANCOVA's, we relied entirely on the Type IV sums of squares and associated *F*-ratios and probabilities that GLM produces. These probabilities tend to be more conservative than traditional Type I or II approaches, and they alone incorporate the distribution of data among effect cells into the design of the model to be tested. For all regressions, the slopes (m) and y-intercepts (b) are presented from the general linear equation for a dependent variable (y) on an independent variable (x): $y = mx + b$. A slope of zero indicates no relation between the independent and dependent variables, and the probabilities that the slope equals zero [$P(m=0)$] also are reported.

TABLE 1. Estimated numbers of breeding pairs of Great Blue Herons and Great Egrets at Audubon Canyon Ranch.

Year	Herons	Egrets
1967	50	70
1968	62	74
1969	55	86
1970	50	85
1971	44	85
1972	46	96
1973	58	99
1974	48	96
1975	45	85
1976	40	65
1977	41	84
1978	43	88
1979	35	98
Mean	47	85

For many analyses R^2, the proportion of the total variance in the dependent variable that is explained by the specified independent variables, provides a convenient indication of the strength of a relationship. Especially in large samples of data, an independent variable can have a highly significant effect (low P) without explaining a very large proportion of the total variance in the dependent variable (low R^2). The calculation of 95% confidence intervals for graphic presentation of some of the data followed the methods of Sokal and Rohlf (1981) with probabilities from Rohlf and Sokal (1981). Means are presented in the text ± 1 SE.

Unless indicated otherwise, the analyses are based on a sample of 729 egret nests and 297 heron nests of known clutch and brood size.

RESULTS

Number of breeding pairs.—The estimated number of breeding pairs of herons during the years of the study ranged between 35 and 62 ($\bar{x} = 47$; Table 1); the estimated number of breeding pairs of egrets ranged from 65 to 98 ($\bar{x} = 85$).

Clutch size.—The overall mean Great Blue Heron clutch size was 3.16 ± 0.04, with a range

TABLE 2. Great Blue Heron clutch size and fledgling production.

			Clutch size												
			1		2		3		4		5				
Year		Mean clutch	*n*	Fledged/ nest	*n*	Fledged/ nest	*n*	Fledged/ nest	*n*	Fledged/ nest	*n*	Fledged/ nest	Total clutches	Total fledged	Fledged/ nest
1967	Successful nests				1	2.00	6	1.83	4	2.50	1	2.00	12	25	2.08
	All nests	3.26			3	0.67	15	0.73	8	1.25	1	2.00	27		0.93
1968	Successful nests				1	2.00	10	2.10	7	2.00			18	37	2.06
	All nests	3.35			1	2.00	11	1.91	8	1.75			20		1.85
1969	Successful nests				2	1.50	10	2.60	10	2.80			22	57	2.59
	All nests	3.33			2	1.50	12	2.17	10	2.80			24		2.38
1970	Successful nests						8	2.25	7	2.00			15	32	2.13
	All nests	3.24	1	0.00	2	0.00	12	1.50	10	1.40			25		1.28
1971	Successful nests				3	1.67	6	1.83	3	3.33			12	26	2.17
	All nests	2.72	1	0.00	7	0.71	11	1.00	3	3.33			22		1.18
1972	Successful nests				1	2.00	7	2.43	6	2.67			14	35	2.50
	All nests	3.24			2	1.00	9	1.89	6	2.67			17		2.06
1973	Successful nests				1	2.00	14	1.93	3	2.00			18	35	1.94
	All nests	3.14			2	1.00	26	1.04	7	0.86			35		1.00
1974	Successful nests				2	1.50	12	2.17	5	2.40			19	41	2.16
	All nests	3.09			3	1.00	14	1.86	5	2.40			22		1.86
1975	Successful nests						3	1.67	7	2.43			10	22	2.20
	All nests	3.23			2	0.00	16	0.31	8	2.13			26		0.85
1976	Successful nests				5	1.60	6	2.33	5	2.60			16	35	2.19
	All nests	3.10			5	1.60	8	1.75	7	1.86			20		1.75
1977	Successful nests						9	1.87	2	2.00			11	21	1.91
	All nests	3.00			2	0.00	17	1.00	2	2.00			21		1.00
1978	Successful nests				2	2.00	8	1.75	5	2.00			15	28	1.87
	All nests	3.10			3	1.35	12	1.17	5	2.00			20		1.40
1979	Successful nests						11	2.45	3	3.33			14	37	2.64
	All nests	3.33					13	2.07	4	2.50	1	0.00	18		2.06
Total	Successful nests				18	1.72	110	2.13	67	2.45			196	431	2.20
	All nests	3.16	2	0.00	34	0.91	176	1.33	83	1.98	2	1.00	297		1.45
Fledged/ egg	Successful nests					0.86		0.71		0.61		0.40			
	All nests			0.00		0.45		0.44		0.49		0.20			

of 1-5 eggs (Table 2). Yearly means ranged from 2.72 in 1971 to 3.35 in 1968. Means were relatively constant from 1967 through 1970. After a marked decline in 1971, they fluctuated irregularly through 1978 and returned to the pre-1970 level in 1979 (Fig. 2). An ANCOVA (R^2 = 0.11) revealed a weak but significant effect of both year ($F_{12,283} = 1.77$, $P = 0.05$) and relative time of breeding ($F_{1,283} = 17.11$, $P = 0.0001$) on heron clutch size. A regression of clutch size on the percent-ranked date of egg-laying revealed a weak decline in clutch size with relative time of breeding [$R^2 = 0.04$, $b = 3.58$, $m = -0.61$, $P(m{=}0) = 0.0004$]. A similar regression for clutch size vs. absolute time of breeding revealed a similarly weak decline [$R^2 = 0.05$, $b = 3.67$, $m = -0.006$, $P(m{=}0) = 0.0001$].

The overall mean Great Egret clutch size was 2.87 ± 0.03 with a range of 1-6 eggs. Annual means ranged from 2.70 in 1970 to 3.07 in 1979 (Table 3). Egret clutch size declined from 1967 through 1970 and increased irregularly in the years following (Fig. 3). An ANCOVA (R^2 = 0.05) revealed a weak but significant effect of both year ($F_{12,715} = 2.25$, $P = 0.009$) and relative time of breeding ($F_{1,715} = 14.61$, $P = 0.0001$) on egret clutch sizes. A regression of clutch size on the percent-ranked date of egg-laying revealed a weak decline in clutch size with relative time of breeding [$R^2 = 0.02$, $b = 3.16$, $m = -0.43$, $P(m{=}0) = 0.002$]. A similar regression for clutch size vs. absolute time of breeding revealed a similarly weak decline [$R^2 = 0.02$, $b = 3.32$, $m = -0.004$, $P(m{=}0) = 0.0001$].

Fledging success.—The mean number of young fledged from all Great Blue Heron nesting attempts was 1.45 ± 0.06 (Table 2). Yearly means ranged from 0.85 in 1975 to 2.38 in 1969 without showing any consistent trend (Fig. 2). An ANCOVA ($R^2 = 0.35$) of fledglings produced per nest vs. clutch size, year, relative time of breeding, and appropriate interaction terms revealed a significant effect of clutch size ($F_{4,252} = 2.88$, $P = 0.02$), year ($F_{12,252} = 4.26$, $P = 0.0001$) and relative time of breeding ($F_{1,252} = 4.43$, $P = 0.04$). A regression of fledglings produced/nest vs. percent-ranked time of breeding revealed a poorly defined decline in fledging success with season [$R^2 = 0.03$, $b = 2.11$, $m = -0.89$, $P(m{=}0) = 0.0048$].

The mean number of fledglings produced/nest for Great Egrets was 0.90 ± 0.04 (Table 3). Yearly means ranged from 0.03 in 1975 to 2.04 in 1979. An ANCOVA ($R^2 = 0.32$) of fledglings produced/nest vs. clutch size, year, relative time of breeding, and appropriate interaction terms revealed a significant effect of only year ($F_{12,672} = 3.04$, $P = 0.0004$). Great Egret fledging success declined from 1967 through 1970, improved somewhat during the following 4 yr, and plunged in 1975 (Fig. 3) due to heavy predation. Success recovered in 1976, and in 1978 and 1979 it exceeded that in all other years.

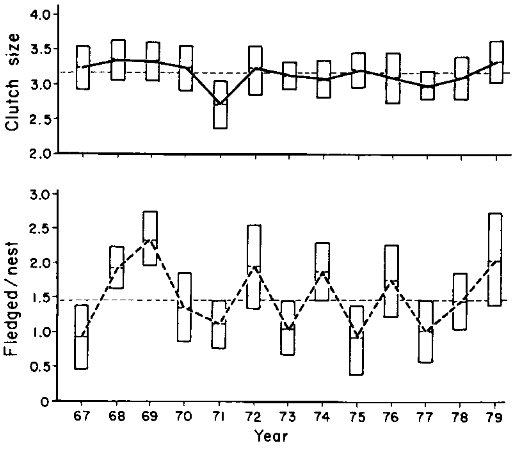

Fig. 2. Annual mean clutch size and fledging success of Great Blue Herons. Rectangles represent 95% confidence intervals. The horizontal line indicates the overall mean. Interyear differences are significant ($P \le 0.05$) where confidence intervals do not overlap. Yearly means differ significantly from the overall mean where it does not cross the confidence interval.

In successful nests only, the number of young fledged increased with clutch size for both Great Blue Herons (Table 2) and Great Egrets (Table 3). The most productive clutch size for both species was 4.

None of the clutches of 1 was successful for either species. These appeared to be incomplete clutches and, when observed, the birds usually were standing. They seldom settled in incubating position. These eggs often were abandoned with dissolution of the pair bond or were started so late in the season that no more eggs were laid.

None of the 7 egret clutches of 5 or 6 was successful; 1 hatched 1 egg, and the others were incubated well past the normal incubation period without hatching.

Overall, 46.8% of Great Blue Heron eggs (n = 910) fledged young. An ANCOVA ($R^2 = 0.31$) analyzing the effect of clutch size, relative time of breeding, year, and appropriate interaction

TABLE 3. Great Egret clutch size and fledgling production.

			Clutch size														
			1		2		3		4		5		6				
Year		Mean clutch	*n*	Fledged/ nest	*n*	Fledged/ nest	*n*	Fledged/ nest	*n*	Fledged/ nest	*n*	Fledged/ nest	*n*	Fledged/ nest	Total clutches	Total fledged	Fledged/ nest
1967	Successful nests				6	1.50	10	2.00	5	2.20					21	40	1.90
	All nests	2.95			8	1.13	26	0.77	6	1.83					40		1.00
1968	Successful nests				3	1.33	11	1.55	4	2.25					18	30	1.67
	All nests	2.80	1	0.00	15	0.27	21	0.81	6	1.50	1	0.00			44		0.68
1969	Successful nests				2	1.00	10	2.20	5	3.00					17	39	2.29
	All nests	2.71	6	0.00	15	0.13	28	0.79	8	1.88	1	0.00			58		0.67
1970	Successful nests				3	1.33	16	2.00	4	2.00					23	44	1.91
	All nests	2.70	5	0.00	25	0.16	42	0.76	10	0.80					82		0.54
1971	Successful nests				2	1.00	23	2.04	3	2.33					28	56	2.00
	All nests	2.85	2	0.00	17	0.12	48	0.98	6	1.17	2	0.00			75		0.75
1972	Successful nests				5	1.60	26	2.00	8	2.38					39	79	2.03
	All nests	2.95			14	0.57	34	1.53	11	1.73					59		1.34
1973	Successful nests				5	2.00	23	1.96	4	1.75					32	62	1.94
	All nests	3.03			12	0.83	44	1.02	11	0.64			1	0.00	68		0.91
1974	Successful nests				4	1.75	26	2.38	3	2.67					33	77	2.33
	All nests	2.98			7	1.00	44	1.41	6	1.33					57		1.35
1975	Successful nests						1	2.00							1	2	2.00
	All nests	2.82	1	0.00	18	0.00	43	0.05	5	0.00			1	0.00	68		0.03
1976	Successful nests				1	2.00	11	2.00	1	3.00					13	27	2.08
	All nests	2.94			3	0.67	28	0.79	1	3.00					32		0.84
1977	Successful nests				7	1.43	15	1.60	2	2.00					24	36	1.50
	All nests	2.71	3	0.00	18	0.56	32	0.75	5	0.49	1	0.00			59		0.61
1978	Successful nests				3	1.67	25	2.08	4	2.50					32	67	2.09
	All nests	3.02			3	1.67	34	1.53	4	2.50					41		1.63
1979	Successful nests				5	2.00	25	2.44	8	2.88					38	94	2.47
	All nests	3.07	1	0.00	6	1.67	28	2.18	11	2.09					46		2.04
Total	Successful nests				46	1.59	222	2.06	51	2.39					319	653	2.05
	All nests	2.87	19	0.00	161	0.45	452	1.01	90	1.36	5	0.00	2	0.00	729		0.90
Fledged/ egg	Successful nests					0.79		0.69		0.59							
	All nests					0.23		0.34		0.34							

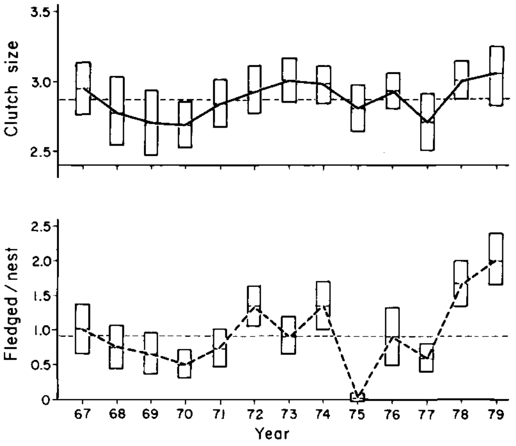

Fig. 3 Annual mean clutch size and fledging success of Great Egrets. Rectangles represent 95% confidence intervals. The horizontal line indicates the overall mean. Interyear differences are significant ($P \leq 0.05$) where confidence intervals do not overlap. Yearly means differ significantly from the overall mean where it does not cross the confidence interval.

terms on the proportion of fledglings produced/egg revealed significant effects of clutch size ($F_{4,243} = 2.56$, $P = 0.04$), relative time of breeding ($F_{1,243} = 6.38$, $P = 0.01$), and year ($F_{12,243} = 3.44$, $P = 0.0001$). A regression of the proportion of fledglings produced/egg vs. the percent-ranked time of breeding revealed a poorly defined decline with season [$R^2 = 0.02$, $b = 0.61$, $m = -0.21$, $P(m{=}0) = 0.0374$].

Great Egrets fledged young from 33.0% of their eggs ($n = 2{,}090$). An ANCOVA ($R^2 = 0.29$) analyzing the effect of clutch size, relative time of breeding, year, and appropriate interaction terms on the proportion of fledglings produced/egg revealed a significant effect only of year ($F_{12,671} = 3.12$, $P = 0.0003$).

Timing of laying.—The earliest heron breeding seasons started with laying of the first egg on 13 February in 1970 and 1971; the latest started with the first egg on 29 February in 1976. Mean clutch initiation dates for the herons varied within a 25-day range from 7 March in 1970 to 31 March in 1971 and 1975 (Fig. 4). The overall mean was 21 March.

Annual variability in clutch initiation was greater for the egrets (Fig. 5) than for the herons. The earliest egret clutch was started on 15 March 1970, and the latest season started on 29 April 1977. The mean egret clutch initiation date was 30 April with a 42-day range across annual means from 14 April 1978 to 25 May 1977.

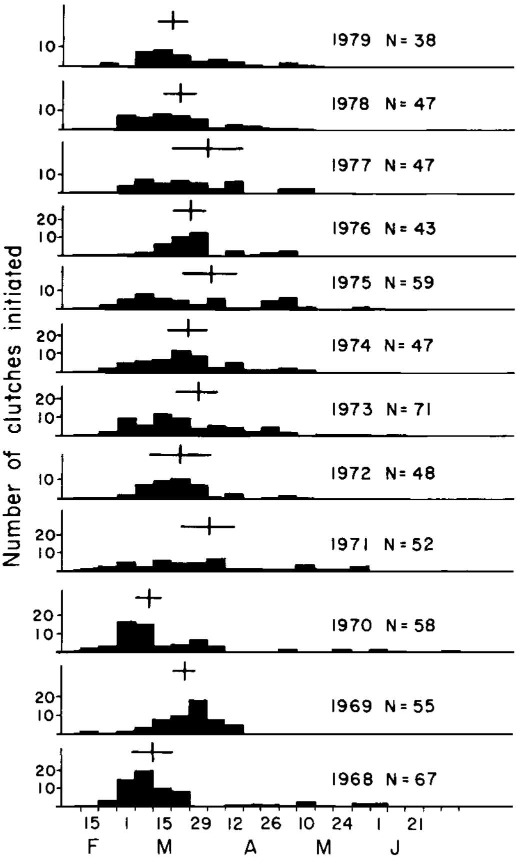

Fig. 4. Frequency distribution for Great Blue Heron clutch initiations. Means (vertical lines) and 95% confidence intervals (horizontal lines) are plotted above each histogram. The year 1967 is not included because observations began in March of that year, after most clutches had been started and too late for accurate dating.

In general neither species was highly synchronous in laying. Heron clutch initiation in 1971 was unusually asynchronous (Fig. 4). Laying synchrony for the egrets was lowest in 1967 (Fig. 5), probably because many rainy days in April of that year (Pratt 1970) depressed egret nesting activities and resulted in a slow "breakthrough" effect (Gochfeld 1980). Late arrivals overlapping with renestings contributed to the extended nesting season.

Effects of the pesticide ban.—Before 1972, when DDT was legal to use, the Great Egrets at Audubon Canyon Ranch lost many eggs due to

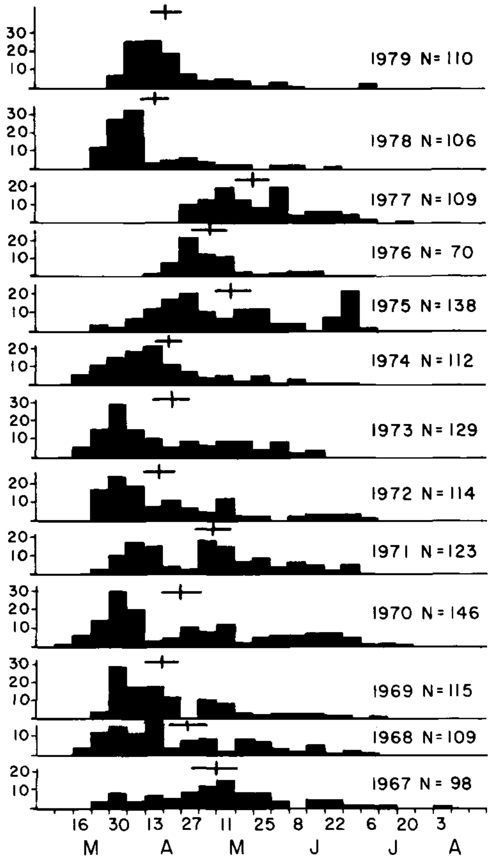

Fig. 5. Frequency distribution for Great Egret clutch initiations. Means (vertical lines) and 95% confidence intervals (horizontal lines) are plotted above each histogram.

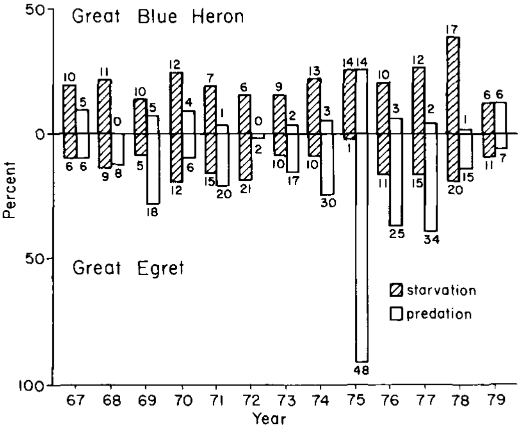

Fig. 6. Percentage of Great Blue Heron and Great Egret young lost to starvation and predation. Numbers above and below bars are sample sizes.

pesticide-induced shell thinning (Faber et al. 1972, Pratt 1972a). To test for changes in egg loss and nesting success after the ban on DDT, the years 1967-1972 were pooled and compared with mean clutch size, brood size, and clutch initiation dates for the years 1973-1979. Mean egret clutch size for 1967-1972 was 2.81 ± 0.04 ($n = 353$), whereas mean clutch size for 1973-1979 was 2.93 ± 0.03 ($n = 363$; for the comparison: $t = 2.22$, $P = 0.0270$). Mean brood size for 1967-1972 was 2.35 ± 0.06 ($n = 193$), and from 1973-1979 it was 2.57 ± 0.05 ($n = 258$; $t = 2.70$, $P = 0.007$). Mean clutch initiation date for 1967-1972 was 29 April ± 1.56 ($n = 353$) and for 1973-1979 it was 2 May ± 1.44 ($n = 363$; $t = 1.21$, $P = 0.23$). Thus, clutch size and brood size increased significantly after the ban on DDT, but mean laying dates were not affected.

Although Great Blue Herons suffered shell thinning during the DDT era, they lost fewer eggs, and reproductive success apparently was not affected (Faber et al. 1972, Pratt 1972a). Heron clutch size was 3.18 ± 0.06 before 1973 ($n = 130$) and 3.14 ± 0.05 after ($n = 158$; $t = 0.57$, $P = 0.57$), brood size was 2.79 ± 0.08 before ($n = 107$) and 2.81 ± 0.08 after ($n = 129$; $t = 0.19$, $P = 0.85$), and mean clutch initiation date was 20 March ± 2.24 before ($n = 130$) and 24 March ± 1.83 after ($n = 158$; $t = 1.43$, $P = 0.16$). Thus, there was no significant difference in heron clutch size, brood size, or laying dates associated with the ban on DDT.

Effect of predation vs. starvation.—Although predation was nocturnal and attacks rarely witnessed, circumstantial evidence for repeated predation by Great Horned Owls (*Bubo virginianus*) and raccoons (*Procyon lotor*) was strong. J. Kipping (pers. comm.) discovered a Great Horned Owl one morning eating a young heron on the ground beneath a nest. In addition, M. Schwartz (pers. comm.) found an owl feather stuck to a clump of bloody egret feathers from a kill of the previous night. Great Horned Owls have been implicated in predation at other heron colonies as well (Cottrille and Cottrille 1958, Callahan and Carey 1979). In 1975, when it was obvious from bloody bodies of egret chicks in the nests that predation was almost completely destroying egret production,

Fig. 7. Mortality of Great Blue Heron chicks per week. Open = starved, hatched = preyed upon, shaded = other.

Fig. 8. Mortality of Great Egret chicks per week. Open = starved, hatched = preyed upon, shaded = other.

observers on the night watch of 20 June saw a raccoon invade nests of both herons and egrets. By morning all nests in that section of the colony were destroyed (Pratt MS). Lopinot (1951) also witnessed raccoon predation on Great Blue Herons, and raccoons have been suspected of predation in ardeid colonies by Teal (1965), Taylor and Michael (1971), and Hjertaas (1982).

Loss of young to predation and starvation varied from year to year for both species (Fig. 6). Herons were more likely to lose chicks to starvation than predation. In a sample of 243 heron nests with known clutch and brood size, 65% of the 672 chicks fledged, 20% starved, predators took 7%, and 7% were lost to other causes. In 453 egret nests with known clutch and brood size, 58% of the 1,124 chicks fledged, 13% starved, predators took 21%, and 8% were lost to other causes.

Age of chick death.—The second through fourth weeks of life were the most hazardous for chicks of both species. Of the 233 heron chicks that died, 76% died during this period (Fig. 7), with greatest mortality occurring in the second week. Of the 471 egret chicks that died, 70% died in the second through fourth weeks (Fig. 8), with greatest mortality in the third week.

DISCUSSION

This study revealed significant reversals in trends in timing of breeding, reproductive success, and to a lesser extent, clutch size of Great Blue Herons and Great Egrets that would not be apparent in short-term studies. In addition, it was apparent that ecological factors affecting reproduction varied among years and between the two species.

The greater susceptibility of heron chicks to starvation suggests that the adult herons had more difficulty finding sufficient food to raise their young than the egrets. There are no data on prey availability for the herons and egrets at Audubon Canyon Ranch, but judging by the agreement between percents of eggs raising young for this study and most others reporting this measure of success (Table 4), food available to the herons at Audubon Canyon Ranch was not unusually limited. Gill's (1973) egg success of 59% may be an overestimate because he found it necessary to limit observations to minimize disturbance.

The greater susceptibility of egret chicks to predation was unexpected. The only known predators on the Audubon Canyon Ranch colony were Great Horned Owls and raccoons. Both Golden Eagles (*Aquila chrysaetos*) and Bald Eagles (*Haliaeetus leucocephalus*) are known predators on Great Blue Herons (Carnie 1954, Bayer 1979, Kelsall and Simpson 1980), but they are rare winter visitants at Audubon Canyon Ranch and to date have not been observed to prey on either species there. Perhaps the smaller size of egret young compared to the herons increased their attractiveness to owls. Marti (1974) reported a mean prey size for Great Horned Owls in Colorado of 177 g, although the maximum was in excess of 2,500 g. Heron eggs start to hatch in March, a month or more before the egret eggs. By late April, when owls in central California are feeding young (J. Winter pers. comm.), young herons would be more than 4 weeks old and weigh 1,500 g or more (McAloney 1973, Merritt 1981). Egret chicks would reach maximum weights of 600–1,000 g (Tomlinson 1976) in mid-June or later. Egret young also might have been at greater risk because they are white and more conspicuous than herons. However, owls are able to see mice in very low light levels (Marti 1974), and it is

TABLE 4. Clutch size and reproductive success reported for Great Blue Heron colonies.

Location	Latitude (°N)	Years	Clutch size	Successful eggs (%)	Fledged/ nest	Fledged/ successful nest	Fledged/ pair	Source
Southern Alberta	49–55	1967–1968	5.00	—	—	2.2–2.5	—	Vermeer (1969)
British Columbia	49	1977–1979	—	—	—	2.3–2.9	—	Kelsall and Simpson (1980)
Idaho	47	1977–1978	—	—	—	2.20	1.95	Collazo (1981)
Idaho	47	1977–1978	—	—	0.5–2.5	2.6–3.4	—	Warren (1979)
Columbia River	46	1978	4.45–4.49	41–50	1.88–2.29	2.29–2.79	—	Blus et al. (1980)
Western Oregon	42–46	1974	—	—	—	2.18–2.70	—	Werschkul et al. (1977)
Nova Scotia	45	1971	4.17	—	—	3.09	2.84	McAloney (1973)
Central Oregon	45	1975	—	—	2.17–2.71	—	1.96	English (1978)
Western Oregon	44	1970	4.19	—	—	2.61	2.04	Henny and Bethers (1971)
Lake Erie	42	1974–1975	3.39	—	2.27	2.46	—	Edford (1976)
Central California	38	1971	3.36	59	2.14	2.50	—	Gill (1973)
Central California	38	1967–1973	3.0–3.7	—	—	1.8–2.3	1.3–2.0	Pratt (1974)
Central California	38	1967–1979	3.16	46.8	1.45	2.20	—	This study
Texas	28	1979	3.58	45	—	—	1.6	Mitchell (1981)
Florida Bay	28	1981	2.88–3.50	—	1.55–2.04	—	—	Powell (1983)

doubtful that herons would be protected by their dark coloration. Heron chicks probably were less affected than egret chicks in 1975 because the raccoons did not invade the colony until June. By this time some young herons had left, and many of those that remained were old enough to escape by hopping across branches. Egret chicks were younger and were more likely to stay huddled in their nests.

The effect of predation at other Great Blue Heron colonies has not been quantified, but reports suggest that its effect on reproductive success has been minor (Lopinot 1951, Bayer 1979, Kelsall and Simpson 1980). Teal (1965) reported losses of Great Egret young to predators of 11%. Comparable data for other Great Egret colonies is unavailable, but in single-year studies at mixed-species colonies predation has resulted in total or near-total loss of young (Dusi and Dusi 1968, Taylor and Michael 1971).

The Great Blue Heron breeding population showed a decline from 1973 onward (Table 1) that was not matched by a similar decline in reproductive success (Fig. 2). We found no relationship between heron population fluctuations and reproductive biology in the same or preceding years. Egret population levels increased annually, except for a sharp temporary decline in 1976 (Table 1). This decline may have been a reaction to the devastating predation in 1975. Members of the heron family are known for colony and individual shifts in breeding locations (e.g. Thompson and Littlefield 1979, Kelsall and Simpson 1980), and our results suggest that predation may prompt a move to another breeding site. However, renesting at the same colony is also recorded (Taylor and Michael 1971).

The seasonal decline in mean clutch size for both species would be expected in light of the tendency for clutch size to decrease with season in all birds (e.g. Klomp 1970, Ryder 1980, Winkler and Walters 1983) as well as herons in particular (Jenni 1969, Wolford and Boag 1971, Siegfried 1972, Rodgers 1980a, Custer et al. 1983a). Several aspects of reproductive biology are associated with this trend, including later breeding by younger birds whose clutches tend to be smaller (e.g. Johnsgard 1973, Ryder 1980), smaller replacement clutches by individual females (e.g. Batt and Prince 1979), and possible genetic control of clutch size and laying date interacting with proximate environmental factors (e.g. Batt and Prince 1979). Data relevant to any of these possibilities at Audubon Canyon Ranch are not available.

The mean clutch sizes reported here are somewhat smaller than those in Pratt (1974) because the sample is larger and includes incomplete clutches of 1 and clutches of 2 that formerly were excluded because they were considered incomplete. Henny's (1972) mean clutch size of 3.66 eggs for Great Blue Herons in central California was based on museum collections, and because egg collectors may have ignored small clutches in favor of larger ones, this measure could be biased toward larger clutches. However, Gill (1973) reported a mean clutch size of 3.63 at a south San Francisco Bay colony in 1971.

Great Blue Heron clutch size was larger during the first 4 yr, declined in 1971 significantly below the overall mean, and returned in 1979 to the level of the first 4 yr (Fig. 2). Great Egret clutch size showed a declining trend from 1967 through 1970, probably in response to pesticide contamination, rose through 1974, and was largest in the final 2 yr (Fig. 3).

Heron clutch size varies geographically, usually increasing with latitude (Palmer 1962, Henny and Bethers 1971, McAloney 1973, Rodgers 1980a, Custer et al. 1983a; but see Custer and Osborn 1977, Gladstone 1979). There is also a tendency for heron clutches to be smaller in coastal and marine habitats than at inland colonies (Henny 1972, Maxwell and Kale 1977). Black-crowned Night-Heron (*Nycticorax nycticorax*) clutches have been shown to be larger in the prepesticide years (Ohlendorf et al. 1978, Findholt 1981), although Custer et al. (1983a) found no relationship between clutch size and DDE concentrations. Recent Great Blue Heron clutches in Ohio (Edford 1976) and Texas (Mitchell 1981) were smaller than the means derived from egg collections for those regions reported by Henny (1972), but means in Oregon (Henny and Bethers 1971, Blus et al. 1980) were about the same. In Florida, most Great White Heron clutches were smaller in 1981 than in 1923 (Powell 1983), but herons that supplemented their natural food by soliciting from humans laid clutches equal in size to those in 1923. Further study of clutch-size trends over time in these species are needed to assess the significance of possible long-term trends.

Although clutches of 4 produced the greatest mean number of young for both species, the most frequent clutch size in both was 3. In most other studies of herons, clutches larger than the mode have been most productive (Millstein et al. 1970; Tomlinson 1975; Morrison and Shanley 1978; Rodgers 1980a, b; but see St.Clair Raye and Burger 1979). These data contradict a strict interpretation of Lack's (1954, 1968) theory that birds maximize their reproductive potential by raising the largest number of young that the parents can feed and that the most productive clutch size should be the most frequent. Parents of both species obtain progressively less "return for their investment" in successful nests as clutch size increases (Tables 2, 3), and it is likely that modal clutch size is reduced from its most productive in these species in response to optimal working-capacity considerations (e.g. Royama 1966, Drent and Daan 1980). Many other possibilities, especially food supply for the laying female and such life-history strategies as bet-hedging, must be considered (e.g. Winkler and Walters 1983). Because nest failures were not clutch-size dependent, success/egg was about the same for all clutch sizes (Tables 2, 3) when both successful and unsuccessful nests were included. Egg loss as a result of shell thinning may have reduced apparent egret clutch size in 1967–1972 because eggs could have been laid and lost before they were detected by observers, but this effect is likely to be small.

Reproductive success can be expressed as the number of eggs resulting in fledged young, the number of young raised/nesting attempt, the number raised/successful nest, or the number raised/pair or breeding female. The number of eggs fledging young or the number of young raised for each nesting attempt usually understates success/breeding female or pair because renestings are not taken into account. Estimating success can be complicated further when nesting attempts are started and lost between observer visits and thus not detected at all (Erwin and Custer 1982). At Audubon Canyon Ranch investigator disturbance apparently did not affect the colony. Previous estimates of nesting success for this colony thus were based on an estimate of the number of breeding pairs (Pratt 1970, 1972a, b, 1974), but to facilitate comparison with other studies, reproductive success in this paper is expressed as the mean number of young raised/nesting attempt and as the percent success of eggs. The number of young fledged/nesting attempt for the herons was 62–97% of the number raised/breeding pair for 7 yr of this study, and the same for 3 yr; in 1968, 1969, and 1972 the number fledged/nesting attempt was 14–19% greater than the number raised/breeding pair because nests of unknown clutch or brood size were excluded from the statistical analysis. For the egrets the number fledged/nesting attempt was 50–96% of the number raised/breeding pair for 12 yr and the same in 1. Overall, the number fledged/nesting attempt was 96% of the number fledged/breeding pair of herons and 81% of the number fledged/breeding pair of egrets.

The proportion of Great Egret eggs producing young (33.0%) is lower than the 44% reported by Teal (1965) and the 67% reported by Maxwell and Kale (1977) and about equal to the 35% reported by Morrison and Shanley (1978). Results from these other studies are not strictly comparable to those from Audubon Canyon Ranch, however. Maxwell and Kale (1977) considered a nest successful when chicks reached 10 days of age, but at Audubon Canyon Ranch much egret mortality occurred later in nestling life (Fig. 3). Neither Teal (1965) nor Morrison and Shanley (1978) were precise about the fledging-age criterion.

The fact that Great Egret fledging success/egg was not significantly related to clutch size, even though larger clutches in successful nests produced more young, may be due to the relatively great importance in this species of eggshell thinning and predation. The intensity of neither of these factors was related to clutch size. The Great Blue Herons were less seriously affected by shell thinning (Faber et al. 1972) and predation (Fig. 6) and showed a significant relationship between clutch size and fledging success/egg.

The mean number of heron young produced/nest was less than the means reported from most other colonies (Table 4), in part because of smaller clutch size. In addition, more complete coverage at Audubon Canyon Ranch may have enabled detection of more nestling mortality and more unsuccessful nests, thus reducing success/nest. At all locations herons in successful nests raised 2-3 young, with 2 usually the mode.

Over the 13 yr of this study, heron fledging success showed a sawtooth pattern, with significant fluctuations above the mean in 1968, 1969, and 1974, below it in 1973 and 1975, and nearly significant lower success in 1971 and 1977 (Fig. 2).

Estimates of reproductive success necessary to maintain a stable population based on banding returns are available for Great Blue Herons north of 40°N (Henny 1972, Bayer 1981), but band recoveries for more southerly latitudes are too few for reliable estimates. Henny (1972) suggested that because mortality probably decreases with a decrease in latitude, a level of reproduction at Audubon Canyon Ranch of 1.5–1.7 would be adequate to maintain the population. However, he did not adjust his estimates to account for differential survival by region and banding location (Bayer 1981). Thus, his estimate may not be accurate.

Mean fledging success for the Great Egrets of 0.90 (Table 3) was greater than the 0.81/nesting attempt reported by Morrison and Shanley (1978) in Texas. A smaller clutch size of 2.3 eggs in Texas, compared with 2.87 in this study, may contribute to the difference. The difference may be even greater than appears because their visits ceased early due to observer disturbance, and mortality of older chicks may have been missed. Comparable figures for other egret colonies are not available.

Egret fledging success declined from 1967 to 1970 (Fig. 3), with significantly higher success in 1974, 1978, and 1979 and lower success in 1975 and 1977.

The 1971 heron season was notable for the small mean clutch size (Table 2) and for the slow pace of laying (Fig. 4). The tendency for younger birds to lay smaller clutches and to lay later (e.g. Klomp 1970, Ryder 1980, Winkler and Walters 1983) cannot be evaluated as a possible factor because age data for the birds at this colony are not available. However, it seems unlikely that there was a sufficient shift in the age structure of the breeding population for 1 yr to account for the observed effects. Low synchrony is frequently associated with smaller colonies (e.g. Wolford and Boag 1971, Burger 1979). However, the breeding population of 44 pairs of Great Blue Herons in 1971 (Table 1) was near the average of 47 pairs for the 13-yr period. It seems more probable that unknown environmental determinants were responsible for both effects.

Egret clutch initiation showed bimodal peaks in 1971 and 1977 (Fig. 5). Rodgers (1980a) attributed similar bimodal peaks for Little Blue Herons (*Egretta caerulea*) to temporary saturation of nesting territories, which prevented late arrivals from setting up courtship territories. At Audubon Canyon Ranch unused nest sites were plentiful even at peak occupancy. A chance concurrence of late arrivals and renesting may have resulted in the second laying peaks. Heavy nest losses in 1975 resulted in an unusually late peak of renesting (Fig. 5).

Chick survival for both species overall was relatively high after the fifth week (Figs. 7, 8).

However, interyear variability in age-dependent mortality can be considerable. In 1-2-yr studies, the week of greatest heron chick mortality spanned a 1-6-week range (Pratt 1970; Gill 1973; Collazo 1979, 1981). Unusual circumstances can produce high mortality even in the 6-7-week period (Warren 1979). There are few comparable data for the egrets. In contrast to this study, Morrison and Shanley (1978) reported greatest egret mortality during the first 10 days after hatching and none after 20 days.

Despite the isolation provided by nesting up to 30 m above the ground, predation is an important source of chick mortality for the egrets. The effect of food supply on the breeding biology of these two species requires considerable more research, but food appears to limit breeding success in the heron and to a lesser extent in the egret and may have an effect on clutch size in both species.

ACKNOWLEDGMENTS

We thank Steven Stearns and Frank Pitelka for their encouragement in initiating the data analysis. Special thanks are due to Richard Doutt, Lucinda Doutt, Michael Ellis, Jules Evens, Barbara Fearis, Elizabeth Meyers, Woody Nackley, Karen Schwartz, Susanna Smail, and Meryl Sundove, all of whom helped at various times with nest observations. We also thank Gary Page, Thomas Custer, and Range Bayer, who made helpful comments on earlier drafts of the manuscript. Partial funding was provided by grants from the International Council for Bird Preservation and Audubon Canyon Ranch. Additional funding was provided by the Point Reyes Bird Observatory. This is contribution Number 175 of the Point Reyes Bird Observatory.

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The **Frank M. Chapman Memorial Fund** gives grants in aid of ornithological research and also postdoctoral fellowships. While there is no restriction on who may apply, the Committee particularly welcomes and favors applications from graduate students; projects in game management and the medical sciences are seldom funded. **Applications are reviewed once a year and should be submitted no later than 15 January.** Application forms may be obtained from the **Frank M. Chapman Memorial Fund Committee, The American Museum of Natural History, Central Park West at 79th St., New York, New York 10024.**

Dr. David R. Wells was appointed Chapman Fellow for the period June 1984 through December 1984. He is working on an atlas of the distribution and speciation of oriental birds. Current Chapman Fellow Robert E. Bleiweiss has been granted an extension of his Fellow status through December 1984. He is studying systematics and speciation in Andean hummingbird genera.

Chapman grants during 1984, totalling $32,781 with a mean of $537, were awarded to: John G. T. Anderson, cooperative foraging behavior in the White Pelican; Ana Victoria Ayala, observations on the interaction between one species of hummingbird and the flowers it uses as food source in a sub-Andean forest; George Barrowclough, ornithological survey of avifauna of Cerro de la Neblina; Jonathan J. Becker, birds of the late Miocene Love Bone Bed local fauna; Henry Lawrie Bell, composition and foraging behavior of insectivorous birds in mixed-species flocks in montane forests of New Guinea; Robert I. Bowman, a genetic analysis of evolution in Galapagos finches; Charles R. Brown, costs and benefits of coloniality in Cliff Swallows (*Hirundo pyrrhonota*); Kenneth G. Bunch, bolus recovery by Gray Jays; Peter F. Cannell, systematics of the avian orders Coraciiformes and Piciformes and allies based on syringeal anatomy; William Carmen, evolution of non-cooperative breeding in the California Scrub Jay (*Aphelocoma coerulescens californica*); John H. Carothers, microevolution of morphology in the Hawaiian Honeycreeper (*Vestiaria coccinea*); Ralph V. Cartar, can Red Phalarope chicks share post-hatching parental care?; Russell A. Charif, investigation of the function of song matching in mockingbirds (*Mimus polyglottos*); T. M. Crowe, phylogeny of the order Galliformes; C. R. Dickman, diet and prey selection of the Barn Owl in Malaysian oil palm plantations; Euan K. Dunn, census of Roseate Tern (*Sterna dougallii*) population on the Azores; Margaret Elowson-Haley, factors eliciting predator alarm calls in the Florida Scrub Jay; C. Craig Farquhar, breeding ecology of the White-tailed Hawk (*Buteo albicaudatus hypospodius*) in Texas; Peter Crawford Frederick, mating strategies in White Ibis (*Eudocimus albus*); Judy Gradwohl, population stability and rigid territoriality in some insectivorous birds on Barro Colorado Island; Rolf Karl-Heinz Grantsau, field guide to the birds of Brazil; Frederick Pearce Greene, determinants of guild structure among insectivorous birds in the Chiricahua Mountains, Arizona; John Morton Hagan III, colonial nesting in Ospreys; Thomas M. Haggerty, reproductive ecology of Bachman's Sparrow; Sylvia L. Halkin, use of song repertoires by male and female Northern Cardinals; J. Christopher Haney, selection pressures and the evolution of sociality in the White-throated Jay (*Cyanolyca mirabilis*); Russell A. Haughey, investigation of the role of the Western White-winged Dove (*Zenaida asiatica mearnsii*) in the pollination of the saguaro (*Cereus giganteus*); Paul Hendricks, foraging ecology of alpine Water Pipits; Holly H. Hobart, cytosystematics of some Arizona birds; Sylvia Hope, phylogeny of Corvidae; H. A. Isack, biology of the Greater Honeyguide (*Indicator indicator*) with emphasis on guiding behavior; Jan Kalina, socioecology of Black-and-white Casqued Hornbills and their role as seed disperser for tropical rain forest trees; Alan C.

(continued on p. 144)

A SEARCH FOR STABILITY GRADIENTS IN NORTH AMERICAN BREEDING BIRD COMMUNITIES

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ABSTRACT.—To search for the existence of stability gradients in North American breeding land bird communities we operationally defined stability (after Järvinen 1979) as year-to-year persistence in species composition and distribution of species abundances. From the census data for 174 study plots we derived nine indices that estimate the annual variability of species composition, the species abundance distribution, diversity, and breeding density. The resulting matrix of study plot by stability indices was used to estimate the correlation structure of the stability indices. The correlation matrix was, in turn, subjected to a principal components analysis to derive synthetic gradients of variation. We then searched for patterns of variation in these stability gradients associated with either geographic location or habitat type. Three independent principal component axes reproduced most of the variation in the initial data and were interpreted as gradients of variation in species turnover, diversity, and breeding abundance. Thus, the annual stability of community structure apparently responds independently to species and abundance variation. Despite the clarity of the derived gradients, few patterns emerged when the plots were ordinated by either habitat or geographic location. In general, grasslands showed greater annual variation in diversity than forested habitats, and, for some habitats, northern communities were less stable than more southern communities. However, few of these patterns were very strong, and we interpret them cautiously. *Received 9 January 1984, accepted 2 August 1984.*

IN this study we investigate annual patterns and variability in the structure of North American breeding bird communities. Specifically, we are interested in determining whether communities differ in their stability properties and whether observed differences can be associated with gross habitat type or geographic location. In general, we operationally consider a community stable if knowledge of its species composition and abundance distribution in year 1 enables us to accurately predict these same properties in year 2. The more accurate the prediction, the more stable the community is considered to be.

For a considerable period of time ecologists generally believed northern communities to be inherently less stable than more southern communities (e.g. MacArthur 1955, Slobodkin and Saunders 1969). This relationship between latitude and stability was believed to be indirect and partly a function of the underlying relationships between latitude and species diversity, and species diversity and stability (see review by Goodman 1975). The necessity of a causal relationship between diversity and stability has been largely refuted from a mathematical perspective (May 1972), but the results from empirical studies have been equivocal or contradictory (McNaughton 1977, 1978). An additional factor believed to contribute to latitudinal differences in stability is a parallel gradient in seasonality. Northern communities should be composed of species populations that show larger annual fluctuations than their less seasonal, more southern counterparts. However, this contrast in seasonality between northern and southern latitudes also has been challenged (Leigh 1975), and apparently some low-latitude environments may be just as seasonal as high-latitude environments.

Despite a general consensus today that latitudinal gradients in stability and seasonality are weak at best, Järvinen (1979) recently has reported geographical gradients in stability of European breeding bird communities that are correlated with latitudinal differences in environmental predictability and seasonality. Employing data from study plots covering a latitudinal range of 19° (50°–69°N), Järvinen found north Scandinavian communities to be less stable than more southern communities. Järvinen's publication suggested to us that a similar

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analysis of North American breeding bird communities would be of comparative interest and perhaps give some further insights into the apparent contradiction between empirical studies and mathematical theory.

In addition to a geographical analysis of North American breeding bird communities, we were interested in investigating the degree to which stability gradients are associated with habitat type. Recent reports from breeding bird community studies in structurally simple habitats suggest that these communities are highly unpredictable on an annual basis (Wiens and Rotenberry 1978, 1980, 1981; Rotenberry and Wiens 1980). This is in contrast to reports from forested habitats where the communities appear more stable on an annual basis (e.g. Kendeigh 1946, Sanders 1970, Holmes and Sturges 1972, Winternitz 1976). Thus, our a priori expectation was that at least some habitat types could be discriminated on the basis of their stability properties, with stability positively related to increased complexity of the habitat structure, and possibly to species richness as well.

In our investigation the initial goal was to determine if it was possible to identify independent gradients of variation that would allow us to ordinate North American breeding bird communities on the basis of stability differences. Contingent upon identifying such gradients, our goals were (1) to give a biologically meaningful interpretation to the derived gradients, and (2) to determine if these gradients could be associated with either habitat type or geographic location. To derive these gradients of variation we used a variety of statistical models, primarily principal components analysis (PCA). Our data are derived from long-term bird censuses from 174 study areas in the United States and Canada. Our approach is empirical and exploratory—we are searching for any patterns that may be superimposed on the synthetic gradients of variation that we derive from a PCA of the annual census data.

MATERIALS AND METHODS

The data set.—The data set used in our analyses consists of breeding bird census reports from the United States and Canada. A large proportion of these censuses have been published in *American Birds* (formerly *Audubon Field Notes*), but we also extracted much census data from other literature sources and from unpublished accounts. (A complete listing of references for the census data used in this study is available upon request.) Because of the great variability in methods used to study breeding bird populations, we established the following criteria for inclusion (cf. Järvinen 1979): 1) Only censuses of land bird communities were included. 2) The study period had to include at least 3 censuses within a 5-yr period, and at least 2 of these censuses had to have occurred in successive years. 3) The study plot had to be ≥ 9 ha in size. 4) The study plot should not have undergone any appreciable change in habitat during the course of the study. 5) Only censuses involving multiple visits and employing a method in which individual territories were mapped were included.

The data set consists of 174 study plots censused over 3–22 yr. The plots were distributed throughout the United States and Canada and covered a latitudinal range of 44° (27°–71°N) and a longitudinal range of 89° (68°–157°W; Fig. 1). The habitat of each study plot was classified into 1 of 10 general types on the basis of its dominant structural habitat characteristics. For the most part, these classifications follow habitat designations given in *American Birds* (see any recent issue listing Breeding Bird Census reports). Plot data derived from other sources were also classified into these categories. The types recognized were: (1) tundra; (2) desert, beach; (3) marsh, open bog, pond; (4) grassland, prairie, shrub-steppe (hereafter referred to as grassland); (5) mixed habitats (two or more distinct habitat types); (6) brush and scrub forest; (7) coniferous forest; (8) deciduous forest; (9) mixed deciduous-coniferous forest; and (10) urban, residential, cemetery. Additional data extracted for each plot were latitude, longitude, state or province, elevation, plot size, number of census years, and number of census hours (when available). Several of these variables acted as covariables in our analyses, and knowledge of them allowed us to statistically control for their influence on the stability indices and facilitated across-plot comparisons.

Stability indices.—In general we followed the operational definition of stability and the computational procedures for analysis of Järvinen (1979: 56). Starting with a census made in a bird community in a certain year, Järvinen considered "community X stabler than community Y if it is, on the basis of census results from X and Y, easier to predict the following properties of X next season than the same properties of Y": (1) total number of pairs on the plot (N), (2) species richness (number of breeding species = S), (3) species diversity (H'), (4) the evenness component of H' (J), (5) species composition, and (6) relative abundance of species present.

To estimate community stability, we calculated several indices for each study plot. The characteristics of several of these indices are discussed in detail by Järvinen (1979), and we will not elaborate on them here. We have added some additional indices, primarily to estimate the predictability of species com-

DISTRIBUTION OF CENSUS PLOTS BY STATE OR PROVINCE

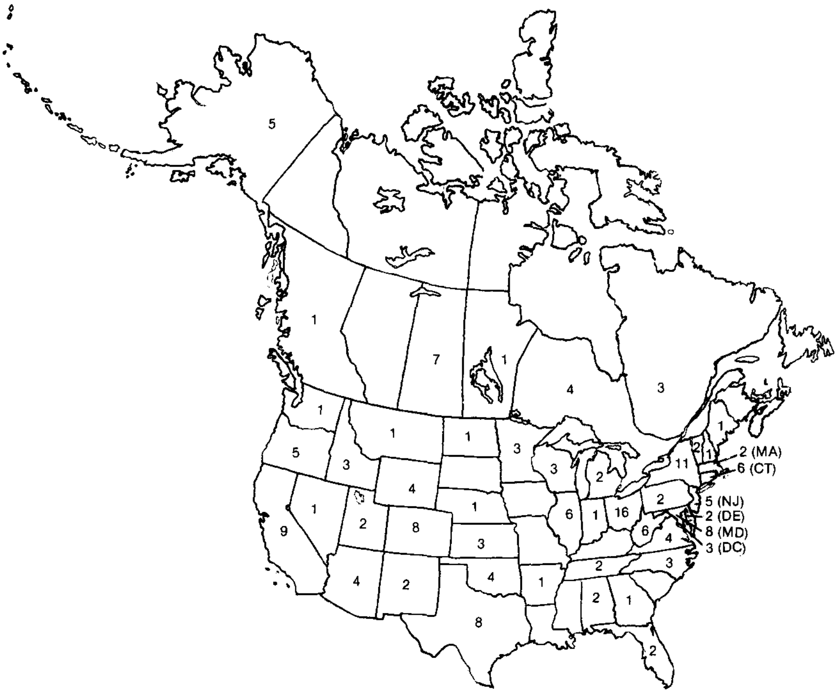

Fig. 1. Geographical distribution of the breeding bird census plots by state or province.

position and relative abundance patterns. The indices used in this study are indicated in Table 1.

Indices 5-9 (Table 1) are calculated only on census data from successive years because they vary as a function of census interval (see Järvinen and Väisänen 1976, Diamond and May 1977). This approach was necessary to assure comparability of across-plot comparisons. For index 3, CV(H'), we initially used the correction for H' as suggested by Hutcheson (1970). However, we found that H'-corrected values gave unrealistic diversity indices for study plots with few species, low overall diversity, and at least one very rare species.

Stability indices were calculated separately for each of the 174 plots, making the individual study plot the basic unit of the analysis. Indices were calculated using the actual number of territories reported for each study plot. Census results were not extrapolated to a constant area because of the problems inherent in this process (Verner 1981) and because we performed no direct between-plot comparisons based on the original data. If fractional territories were reported, we only considered species with ≥ 0.1 territory when calculating the indices T and $P(E)$. Analyses were run with larger cutoff values, but these had no effect on the final results. By including fractional territories, the number of colonizations and extinctions may be overestimated. However, our purpose here is not to accurately estimate the true turnover values but rather to ordinate plots according to their relative turnover values.

All species included in the original censuses were retained for our analyses. We examined the effect of eliminating raptor and waterfowl species from the calculations, and these changes had no effect on the final results.

Many of the stability indices were not normally distributed, largely because of outlying points. However, in no case was the deviation from normality excessive. Rather than adjusting for outliers by transformation, we investigated their influence on the multivariate analyses directly. Outliers were identified by differences in the Mahalanobis distances between each plot and the grand centroid of all plots in factor space relative to observation space. The inclusion or exclusion of outliers identified by this method had little effect on the plot ordinations or on our final interpretations.

It is clear that few of the stability indices vary independently from any of the other indices (see Järvinen 1979 and further discussion below). However, prior to any formal analyses, the indices suggest a logical partitioning of the matrix X into subsets that are sensitive to different sources of variation in avian

TABLE 1. Indices used in the stability analysis.

Index number and symbol	Description
(1) CV(N)	Coefficient of variation of breeding abundance, where CV(N) = (σ/m), σ = standard deviation of N, and m = mean of N
(2) CV(S)	Coefficient of variation of species richness
(3) CV(H')	Coefficient of variation of species diversity, where $H' = -\Sigma p_i \ln p_i$, $p_i = n_i/N$, and n_i = the number of individuals in the ith species
(4) CV(J)	Coefficient of variation of the evenness component of H', where $J = H'/\ln S$
(5) $\overline{T}$	Average species turnover, measured as the arithmetic average of the index (see Lynch and Whitcomb 1977): $T = (I + E)/(I + E + S_c)$, where I and E are the number of species that have immigrated and gone extinct, respectively, between two successive annual censuses and S_c is the number of species in common between two successive censuses
(6) $\overline{CC}$	Average coefficient of community, measured as the arithmetic average of the index (Sorensen 1948): $CC = 2S_c/(S_1 + S_2)$, where S_c is as defined above, S_1 = the estimated number of species in census 1, and S_2 = the estimated number of species in census 2
(7) $\overline{rD}$	Average change in community composition, measured as the arithmetic average of the index (Järvinen and Väisänen 1976): $rD = 100(\exp DIV_{\text{diff}} - 1)$, where $DIV_{\text{diff}} = H'_{1+2} - 0.5 \cdot (H_1' + H_2')$. H_1' and H_2' are the diversity indices for the bird community in census periods 1 and 2, and H'_{1+2} is the diversity index derived from pooling the census results across two successive years
(8) $\overline{BC}$	Average Bray-Curtis similarity coefficient (Bray and Curtis 1957) calculated as the arithmetic average between two successive censuses as: $BC = 1 - [\Sigma \lvert n_{i1}^* - n_{i2}^* \rvert / \Sigma (n_{i1}^* - n_{i2}^*)]$, where n_{i1} and n_{i2} are the number of territories of the ith species in censuses 1 and 2, respectively, and $n_{i1}^* = \ln(n_{i1} + 1)$ and $n_{i2}^* = \ln(n_{i2} + 1)$. (See Huhta 1979 for the rationale behind this transformation.)
(9) $\overline{P(E)}$	Average annual extinction probability, calculated as the arithmetic average between two censuses as: $P(E) = 1 - (S_c/S_1)$

community structure. The indices T, $P(E)$, and CC reflect changes in species composition between successive censuses and thus are indicative of species compositional stability. The indices CV(S), CV(J), and CV(H') are sensitive to changes in the distribution of species abundances and species density, but, in theory, can be independent of changes in species composition. These indices thus reflect diversity variation. Indices rD and BC are sensitive to changes in both species composition and the abundance distribution. Unfortunately, the relative influence of these two sources of variation is confounded in these indices. In addition, rD and BC differ from each other in being sensitive to shifts in relative and absolute abundance, respectively. These indices can be interpreted as reflecting overall compositional stability in the breeding bird community. The final index, CV(N), is sensitive to changes in overall breeding abundance and shifts in the abundance distribution and thus reflects annual variation in the number of breeding birds.

Univariate statistical analyses.—Means and standard deviations were calculated, by habitat, for each of the unadjusted stability indices and for $\bar{S}$, $\bar{N}$, and plot size. The abundance of breeding birds is a direct function of area and was controlled by standardizing average abundances to 20 ha, the overall average plot size. The variable S is a function of plot size up to some asymptotic limit that probably varies by habitat type (James and Rathbun 1981). However, estimates of $\bar{S}$ were not adjusted for differences in plot size because they did not covary (see Discussion).

Tests of the null hypothesis of no difference in the means, by habitat, for each stability index and for $\bar{S}$ and $\bar{N}$ were conducted using Welch's ANOVA model (Brown and Forsythe 1974b), which does not assume homogeneity of group variances. Pairwise contrasts were based on Bonferroni confidence intervals and were calculated only after a significant overall ANOVA was found. Separate ANOVA's for each variable are not strictly valid because the variables are not all independent. We calculated them for heuristic purposes only and caution the reader that faulty inferences can be made from such comparisons. We employed correlation models frequently in our analyses. In all cases we computed Pearson product-moment correlation coefficients (Sokal and Rohlf 1981) on untransformed data. Correlation coefficients were calculated only after examining bivariate scattergrams and assuring ourselves of the absence of nonlinear relationships.

Multivariate statistical analyses.—In practice the stability indices do not vary independently of each other. Therefore, we focused on synthetic gradients of variation in the stability matrix X by analyzing the correlation structure of X with principal components analysis (PCA). After initial extraction of the principal components, we rotate the eigenvectors (varimax rotation algorithm) to simplify the pattern of factor loadings and to facilitate interpretation. We are ultimately interested in giving these synthetic gradients a biological interpretation by incorporating our understanding of what the indices measure with their correlation to each component.

We considered the factor scores, partitioned by habitat, separately for each factor by ANOVA. In all cases we tested for equality of the variances by Levene's test (Brown and Forsythe 1974a) and found significant heterogeneity. As a result, we used the Welch ANOVA model to test for differences in the habitat-group means along each factor. When a significant overall ANOVA was found, we tested all possible pairwise combinations of means after adjusting for multiple comparisons by the Bonferroni method and maintaining an experimental error rate at $\alpha = 0.05$.

To clarify how individual habitat types were ordinated along these synthetic gradients, we computed factor scores for each of the plots, partitioned the scores by habitat, and examined them separately for each factor by ANOVA. We excluded three habitat types from further consideration because of small sample size.

Sample size and covariance problems with similarity indices.—Järvinen (1979) discussed some of the statistical difficulties encountered when similarity indices are applied to breeding bird data. In addition, there are unavoidable sampling correlations for several of our annually calculated indices. For example, successive calculations of the CC index both contain the value S_2 in the denominator. Thus, for both biological and statistical reasons some degree of correlation between these indices is inherent in our investigation. We are confident that any biases that are introduced are consistent across plots, and of small magnitude.

A more serious problem has been discussed by Wolda (1981), who showed that several similarity indices are affected by both sample size and diversity of the samples being compared. Wolda's results indicate that the *BC* index has higher expected maximum values for comparisons of large (greater S and N) than of small communities, and higher values for comparisons of communities of similar size. The *CC* index is similarly affected, but to a lesser degree.

To investigate how our stability indices were affected by sample size differences across study plots, we examined the functional relationship between the mean value of each index and $\bar{S}$ and $\bar{N}$ with regression and correlation analyses. Untransformed models as well as transformations of the dependent variable and polynomial functions of the independent variable were employed to maximize fit to the data. For significant models, the effect of $\bar{S}$ or $\bar{N}$ was removed from the index by partial correlation analysis. In these cases only the residuals were retained for subsequent analyses.

The coefficient of variation indices were not adjusted for $\bar{S}$ and $\bar{N}$ because the CV statistic is already normalized for differences between the means of different samples (Lewontin 1966, Sokal and Braumann 1980, Sokal and Rohlf 1981). To illustrate, if we assume that random variables X and Y measure species richness in two habitat types and that the distribution of these two variables are identical except that Y is k times as large as X, then we have the following relationship among the coefficients of variation for these variables (see Lewontin 1966):

$$\text{if } Y = kX, \text{ then } \bar{Y} = k\bar{X} \text{ and}$$
$$S_y^2 = k^2S_x^2, \text{ or } S_y = kS_x.$$

The coefficient of variation of Y is then:

$$\mathrm{CV}(Y) = S_y/\bar{Y} = kS_x/k\bar{X} = \mathrm{CV}(X).$$

Relationship of the stability indices to other covariables.—The relationships between the mean value of each index and the mean values of several covariables (latitude, longitude, elevation, plot size, number of census years) were examined by correlation analyses. Because we wished to focus on patterns of variation dependent as clearly as possible on differences in habitat or geographic location, we removed the linear effects of the covariables from the indices by partial correlation analysis before performing the multivariate analyses. The stability indices were adjusted for all covariables for the habitat analyses, and all covariables except latitude and longitude for the geographic analyses.

Some of the stability indices may be sensitive to differences in sampling effort. To investigate this effect we developed an index of sampling effort defined as the mean number of census hours/plot size (h/ha). We examined the correlation between this index and all of the stability indices.

Estimating the proportion of long-distance migrants.—We arbitrarily defined a long-distance migrant (LDM) as a species that travels ≥1,600 km from its breeding ground to the northern extent of its wintering area. We assumed that mortality due to migration was linearly related to distance traveled and independent of point of departure. Minimum migration distances, computed as the distance from the study plot to the northern edge of the species winter range, were estimated by making reference to range maps in Peter-

TABLE 2. Correlation between each stability index and $\overline{S}$ and $\overline{N}$.[a]

Index	$\overline{S}$	$\overline{N}^{b}$
CV(*N*)	−0.317**	−0.060
CV(*S*)	−0.486**	−0.128
CV(*H′*)	−0.419**	−0.179*
CV(*J*)	−0.524**	−0.029
$\overline{T}$	−0.277**	−0.274**
$\overline{CC}$	0.256**	0.273**
$\overline{rD}$	−0.181*	−0.162*
$\overline{BC}$	0.191*	0.267**
$\overline{P(E)}$	−0.122	−0.221**

[a] * $P \leq 0.05$; ** $P \leq 0.01$.

[b] Standardized to an area of 20 ha.

son (1980) and Robbins et al. (1983). For each plot we determined the average proportion of LDM and investigated the relationship between this variable and each of the stability indices by correlation analysis. In addition, the null hypothesis of no difference in the mean proportion of LDM, by habitat, was tested with the Welch ANOVA model (see earlier discussion). In order to better meet the assumptions of the ANOVA model, the proportion LDM was transformed with the arcsine function prior to conducting the analysis.

RESULTS

Statistical aspects of the stability indices.—Wolda (1981) showed the indices *BC* and *CC* to be rather strongly dependent upon the sample size of the communities being compared over the range of 100–5,000 individuals. However, when calculating mean values within plots our estimates of these indices were insensitive to this problem. This occurs because the samples we compared for similarity were from the same plots in successive years and, consequently, did not differ extensively in number of individuals or in diversity.

However, when examining across-plot comparisons, significant, but weak, relationships were found for both indices when regressed on $\bar{S}$ and $\bar{N}$ (Table 2). The maximum R^2 was <12% for any simple linear regression model. Transformations of the dependent variable to achieve a better model were judged less satisfactory than nontransformed models because of smaller R^2 values. Even a third-order polynomial of the independent variable for the *BC* index only increased the R^2 value from 12% to 16%. When the linear effects of $\bar{S}$ and $\bar{N}$ were removed from the indices *BC* and *CC* to correct for the effects of sample size difference, the residuals showed no linear trends when regressed back on $\bar{S}$ and $\bar{N}$.

The remaining stability indices all had significant correlations with either $\bar{S}$, $\bar{N}$, or both (Table 2). The correlations were particularly strong for the coefficient of variation indices. We did not remove the linear effects of $\bar{S}$ and $\bar{N}$ from these indices because we had no evidence that these relationships were statistical artifacts as opposed to true biological relationships (see below).

Relationship of the stability indices with other covariables.—We were unable to adjust the indices for differences in sampling effort because these data were not available for all plots. However, we were able to compute sampling effort for 131 of the plots, and the maximum correlation between this variable and any of the indices was <0.150 (Table 3). Thus, there is no evidence that differences in sampling intensity biased any of our results. Of the 45 possible bivariate correlations between the re-

TABLE 3. Correlations between the stability indices and the covariables.[a]

Covariable	Stability index								
	CV(*N*)	CV(*S*)	CV(*H′*)	CV(*J*)	$\overline{T}$	$\overline{CC}$	$\overline{rD}$	$\overline{BC}$	$\overline{P(E)}$
Latitude	0.058	0.128	0.055	0.003	0.210*	−0.205*	0.098	−0.160*	0.195*
Longitude	0.008	0.179*	0.113	0.177*	0.125	−0.122	−0.002	0.025	0.025
Elevation	0.071	0.235*	0.180*	0.117	0.170*	−0.177*	0.146	−0.079	0.053
Plot size	0.042	0.034	0.057	−0.012	−0.013	0.017	−0.169*	0.086	−0.072
Number of years	0.059	0.025	−0.086	−0.105	−0.132	0.138	−0.169*	0.170*	−0.083
Sampling effort[b]	−0.117	0.072	0.126	−0.019	0.146	−0.148	0.052	−0.065	0.126

[a] * $P \leq 0.05$; ** $P \leq 0.01$.

[b] Based on a sample size of $n = 131$.

TABLE 4. Means (SD) for each stability index and for $\overline{S}$, $\overline{N}$, plot size, and the proportion of long-distance migrants (LDM) by habitat type.

	Habitat type						
Index	Tundra ($n = 5$)	Grassland ($n = 30$)	Mixed ($n = 9$)	Scrub ($n = 15$)	Conifer ($n = 24$)	Mixed D-C ($n = 22$)	Deciduous ($n = 65$)
CV(N)	0.232	0.262	0.170	0.154	0.216	0.139	0.163
	(0.074)	(0.184)	(0.105)	(0.068)	(0.118)	(0.082)	(0.103)
CV(S)	0.175	0.184	0.118	0.185	0.162	0.121	0.104
	(0.048)	(0.109)	(0.054)	(0.137)	(0.106)	(0.077)	(0.062)
CV(H')	0.062	0.112	0.031	0.121	0.075	0.049	0.042
	(0.022)	(0.088)	(0.020)	(0.193)	(0.067)	(0.033)	(0.026)
CV(J)	0.044	0.079	0.026	0.070	0.033	0.029	0.032
	(0.027)	(0.051)	(0.009)	(0.066)	(0.028)	(0.023)	(0.020)
$\overline{T}$	0.332	0.269	0.233	0.322	0.293	0.268	0.263
	(0.055)	(0.144)	(0.056)	(0.103)	(0.092)	(0.074)	(0.091)
$\overline{CC}$	0.795	0.831	0.864	0.797	0.822	0.842	0.844
	(0.039)	(0.102)	(0.038)	(0.076)	(0.067)	(0.049)	(0.064)
$\overline{rD}$	7.69	6.59	5.78	7.47	9.04	6.97	6.21
	(3.72)	(5.13)	(1.76)	(4.81)	(3.95)	(3.34)	(3.82)
$\overline{BC}$	0.788	0.820	0.833	0.809	0.792	0.811	0.822
	(0.040)	(0.084)	(0.030)	(0.062)	(0.057)	(0.059)	(0.056)
$\overline{P(E)}$	0.189	0.156	0.145	0.170	0.140	0.154	0.153
	(0.058)	(0.100)	(0.060)	(0.105)	(0.062)	(0.050)	(0.068)
$\overline{S}$	14.9	7.3	40.1	14.4	18.3	25.3	27.1
	(2.0)	(5.2)	(9.0)	(8.5)	(8.4)	(6.0)	(8.7)
$\overline{N}$[a]	27.0	117.0	159.9	96.8	125.0	112.0	155.5
	(8.9)	(217.0)	(65.9)	(100.9)	(102.9)	(57.8)	(144.6)
Plot size	60.8	17.3	21.0	18.7	14.9	13.4	17.0
	(40.7)	(9.2)	(10.5)	(10.9)	(6.3)	(4.4)	(9.7)
LDM	0.823	0.179	0.361	0.167	0.259	0.396	0.409
	(0.069)	(0.182)	(0.147)	(0.151)	(0.151)	(0.119)	(0.136)

[a] Standardized to a plot size of 20 ha.

maining covariables and the 9 stability indices, 13 were significant at $P < 0.05$. Only one stability index (rD) was significantly correlated with area ($r = -0.169$, $P < 0.05$).

Geographic and habitat trends in plot size.—Inferences drawn from the multivariate analyses may be influenced by geographic or habitat trends in plot size. The correlations between plot size and latitude and longitude were 0.413 ($P < 0.01$) and 0.301 ($P < 0.01$). However, when tundra plots were removed from the analysis, the correlations became nonsignificant ($r_{\text{lat., plot size}} = -0.022$ and $r_{\text{long.,plot size}} = 0.002$). This dramatic change is a result of the large plot size and extreme geographic location of the tundra study areas. They acted as outliers in the analysis and had a disproportionate effect on the magnitude of the correlation coefficient. Tundra plots were not considered in our geographical analyses (see below).

When the data were partitioned by habitat there was only one significant relationship between geographic position and plot size (scrub forest plots are significantly correlated with longitude, $r = 0.545$). However, the linear effects of both plot size and geographic position were removed from all indices prior to performing the habitat PCA. We thus conclude that our results were not confounded by either geographic or habitat trends in plot size.

Univariate analyses of the stability indices by habitat.—Means and standard deviations, by habitat, for each of the stability indices and for $\overline{S}$, $\overline{N}$, and plot size are reported in Table 4. We report plot size in this table because of the possible bias this may give to comparisons of stability variables and $\overline{S}$ across plots (see Discussion).

The results of significant pairwise comparisons of habitat means for each stability index and $\overline{S}$ and $\overline{N}$ are shown in Table 5. A significant ANOVA was detected for $\overline{CC}$, but there

TABLE 5. ANOVA results from all possible pairwise comparisons of habitat means for each stability index, $\bar{S}$, $\bar{N}$, and the proportion of long-distance migrant species (LDM). Tests are based on Bonferroni confidence intervals and separate variances. Only variables with both significant ANOVA's and a posteriori comparisons are tabulated.[a]

Groups compared	CV(N)	CV(S)	CV(H')	CV(J)	$\bar{S}$	$\bar{N}$[b]	LDM
Tundra vs. grassland					+		+
Tundra vs. mixed					−	−	+
Tundra vs. scrub							+
Tundra vs. conifer						−	+
Tundra vs. mixed D-C					−	−	+
Tundra vs. deciduous					−	−	+
Grassland vs. mixed			+	+	−		
Grassland vs. scrub							
Grassland vs. conifer				+	−		
Grassland vs. mixed D-C	+		+	+	−		−
Grassland vs. deciduous		+	+	+	−		−
Mixed vs. scrub					+		
Mixed vs. conifer					+		
Mixed vs. mixed D-C					+		
Mixed vs. deciduous					+		
Scrub vs. conifer							
Scrub vs. mixed D-C					−		−
Scrub vs. deciduous					−		−
Conifer vs. mixed D-C							−
Conifer vs. deciduous					−		−
Mixed D-C vs. deciduous							

[a] "+" indicates that the first group listed had a significantly larger mean value; "−" indicates that the second group had a larger mean value.

[b] Standardized to an area of 20 ha.

were no significant a posteriori comparisons. The most striking result to arise from these multiple contrasts was that of 189 pairwise comparisons of the indices only 8 were significant. The significant differences suggest that grasslands differ from other habitat types by showing greater annual variation in species diversity, richness, and evenness. Tundra habitats differ from all the others, except grassland and scrub forest habitats, by having significantly lower breeding densities. The most extensive differences between habitats occurred in their average species-richness values. Grassland habitats have significantly lower $\bar{S}$ values than all other habitat types, and mixed habitats significantly higher values. In addition, deciduous forest habitats have significantly larger $\bar{S}$ values than either scrub or coniferous forest habitats.

A search for habitat gradients (PCA I).—The correlation matrix of residuals used as input to the PCA for habitat effects is presented in Table 6. This matrix can be partitioned into three subsets of highly correlated variables: (1) $\bar{T}$*, $\overline{CC}$*,

TABLE 6. Correlations of residual stability indices—habitat analysis.[a]

	CV(S)*	CV(N)*	CV(H')*	CV(J)*	$\bar{T}$*	$\overline{CC}$*	$\overline{rD}$*	$\overline{BC}$*
CV(N)*	0.259							
CV(H')*	0.743	0.275						
CV(J)*	0.467	0.256	0.658					
$\bar{T}$*	0.432	0.019	0.255	0.139				
$\overline{CC}$*	−0.425	−0.054	−0.251	−0.166	−0.960			
$\overline{rD}$*	0.329	0.350	0.269	0.002	0.658	−0.660		
$\overline{BC}$*	−0.299	−0.375	−0.189	−0.022	−0.700	0.746	−0.900	
$\overline{P(E)}$*	−0.220	0.024	0.105	0.010	0.836	−0.814	0.580	−0.603

[a] * = residual stability indices with the linear effects of all covariables removed.

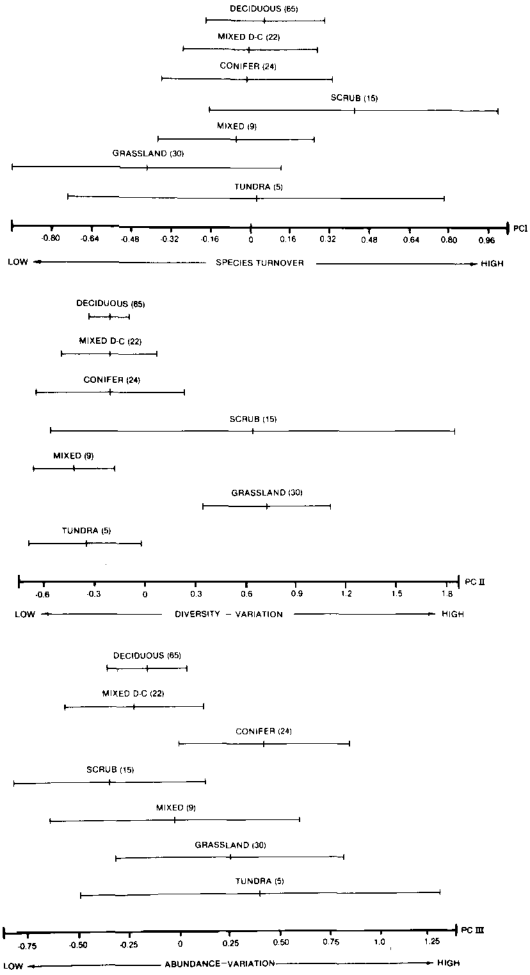

Fig. 2. Ordination of the breeding bird census plots along the first three principal components, partitioned by habitat type. For each habitat type the sample size is given in parentheses, and the mean and 95% confidence interval are illustrated. Axis PCI represents a gradient in species turnover, axis PCII represents a gradient in diversity variation, and axis PCIII represents a gradient in abundance variation.

TABLE 7. Rotated factor loadings—habitat analysis. Dominant factor loadings are in boldface.

	Factor		
Index[a]	I	II	III
$\overline{T}$*	**0.949**	0.205	−0.045
$\overline{CC}$*	**−0.943**	−0.207	0.001
$\overline{P(E)}$*	**0.895**	0.017	−0.053
$\overline{BC}$*	**−0.789**	−0.013	**−0.529**
$\overline{rD}$*	**0.749**	0.046	**0.537**
CV(*H*′)*	0.112	**0.901**	0.154
CV(*J*)*	−0.047	**0.846**	0.036
CV(*S*)*	0.298	**0.798**	0.124
CV(*N*)*	−0.034	0.224	**0.901**
% variance	43.0	25.6	15.8
Cumulative variance	43.0	68.6	84.4

[a] * = residual stability indices with the linear effects of all covariables removed.

*rD**, *BC**, and *P*(*E*)*; (2) CV(*S*)*, CV(*H*′)*, and CV(*J*)*; and (3) CV(*N*)*. These subsets are largely those that one might expect a priori to measure similar aspects of stability.

The percent total variation in the system accounted for by the three factors is >84% (Table 7). Because of the clarity of the factor loadings, we feel we can give meaningful interpretations to the gradients. We interpret factor I (accounting for 43% of the variation) as a species- and individual-turnover gradient, factor II (25.6%) as a diversity-variation gradient, and factor III (15.8%) as an abundance-variation gradient. Factor I is subsequently referred to as a species-turnover gradient, reflecting its dominant factor loadings. Factor III is dominated by CV(*N*) but also has high loadings for indices $\overline{BC}$ and $\overline{rD}$, which are both influenced by changes in the distribution of abundance across species. In fact, Järvinen (1979) referred to *rD* as an index of "average individual turnover."

Graphical display of the mean and variance of each factor by habitat type gives a visual impression of the dispersion of plots along each gradient (Fig. 2). Testing the differences among habitat types separately for each factor by ANOVA is premised on the statistical independence of the factors. However, independence is assured only across the entire sample and may not hold across factors within a given habitat type. We examined this effect and found no significant correlations. As a consequence of an almost complete independence across factors, we proceed with a separate ANOVA for each.

The ordination of plots by habitat type along the species-turnover gradient (factor I; Fig. 2, top) shows no clear pattern. Each habitat type seems to be characterized by extensive variability rather than a strong central tendency. Grassland plots on the average showed the lowest species turnover, scrub forest the highest, with the remaining groups being inter-

TABLE 8. Rotated factor loadings—geographic analysis. Dominant factor loadings are in boldface.

Index[a]	Factor I	 II	 III
$\overline{T}$*	**0.945**	0.214	−0.045
$\overline{CC}$*	**−0.941**	−0.184	0.013
$\overline{P(E)}$*	**0.897**	0.028	−0.047
$\overline{BC}$*	**−0.794**	0.009	**−0.512**
$\overline{rD}$*	**0.764**	0.048	**0.517**
CV(H')*	0.114	**0.897**	0.160
CV(J)*	−0.063	**0.848**	0.028
CV(S)*	0.315	**0.795**	0.121
CV(N)*	−0.015	0.220	**0.908**
% variance	43.5	25.4	15.5
Cumulative variance	43.5	68.9	84.4

[a] * = residual stability indices with the linear effects of all covariables, except latitude and longitude, removed.

TABLE 9. The linear correlation of each factor with latitude and longitude, overall and by habitat.[a]

Habitat	Factor	Correlated with: Latitude	 Longitude
Overall	I	0.217**	−0.002
(n = 174)	II	0.051	0.094
	III	0.026	−0.073
Grassland	I	0.150	−0.170
(n = 30)	II	−0.108	−0.093
	III	−0.198	−0.483**
Mixed	I	−0.005	0.287
(n = 9)	II	0.383	−0.208
	III	−0.124	0.104
Scrub	I	0.548*	0.033
(n = 15)	II	−0.003	0.228
	III	−0.266	−0.265
Conifer	I	0.440*	−0.360
(n = 24)	II	0.470*	−0.314
	III	0.061	−0.259
Mixed D-C	I	0.458*	−0.376
(n = 22)	II	−0.356	−0.235
	III	−0.268	−0.281
Deciduous	I	0.013	0.191
(n = 65)	II	0.204	−0.002
	III	0.073	−0.112

[a] * $P \le 0.05$; ** $P \le 0.01$.

mediate and almost coincident. There were no significant differences among group means on factor I ($F_{6,34} = 0.86$, $P = 0.546$). The relative positions of some habitat groups along this gradient were substantially affected by partialling out the effects of $\bar{S}$ and $\bar{N}$ from the indices $\overline{BC}$ and $\overline{CC}$. For example, the grassland group shifted towards lower turnover and the deciduous group towards higher turnover when residuals were used.

A clearer pattern of ordination occurred along factor II (Fig. 2, middle), where an overall significant difference is evident in the position of habitat means ($F_{6,34} = 5.07$, $P = 0.0008$). Pairwise, a posteriori tests of the equality of habitat means indicated that grassland plots showed significantly higher ($P < 0.005$) diversity variation than tundra, mixed, coniferous, mixed deciduous-coniferous, and deciduous plots. No other comparisons of habitat types showed significant differences.

Factor III suggests some pattern to the relationship between habitat type and abundance stability (Fig. 2, bottom), but no overall significant differences among means were found ($F_{6,32} = 1.91$, $P = 0.11$). Very slight overlap of the 95% confidence intervals of the coniferous and deciduous forest plots suggests a significant difference, but this difference was obviated by holding the experimental error at $\alpha = 0.05$ ($t = -2.56$, $P = 0.015$; critical Bonferroni $P = 0.0024$). A slightly larger sample size may have shown that coniferous forests experience greater abundance variation among years than other forest types.

A search for geographical gradients (PCA II).—The rotated factor loadings resulting from the analysis of the residual correlation matrix controlling for all covariables except latitude and longitude are shown in Table 8. More than 84% of the total variation in the original data is explained by the first three factors. Even though 6 of the 18 correlations between latitude and longitude and the 9 stability indices were significant (Table 3), none were large (maximum $r = 0.210$). As a result, the residual correlation matrix, the derived factor loadings, and our overall interpretation of the factors as gradients in species turnover, diversity variation, and abundance variation are basically unchanged from the previous analysis.

We calculated the linear correlation of each factor with latitude and longitude (Table 9). Over all plots the only significant correlation observed was between factor I and latitude ($r = 0.217$, $P < 0.01$), suggesting that species and individual turnover generally increased from south to north. None of the other correlations suggested even a slight relationship between community stability and geographical location.

TABLE 10. The linear correlation of $\bar{S}$ and $\bar{N}$[a] with latitude and longitude, overall and by habitat.[b]

Habitat	Variable	Correlated with: Latitude	Correlated with: Longitude
Overall	$\bar{S}$	−0.155*	−0.275**
(n = 174)	$\bar{N}$	−0.262**	−0.016
Grassland	$\bar{S}$	0.078	0.044
(n = 30)	$\bar{N}$	−0.299	0.030
Mixed	$\bar{S}$	0.237	−0.312
(n = 9)	$\bar{N}$	0.518	−0.132
Scrub	$\bar{S}$	−0.057	−0.180
(n = 15)	$\bar{N}$	−0.021	−0.058
Conifer	$\bar{S}$	−0.375	0.234
(n = 24)	$\bar{N}$	−0.418*	0.346
Mixed D-C	$\bar{S}$	0.270	0.266
(n = 22)	$\bar{N}$	−0.287	0.398
Deciduous	$\bar{S}$	−0.122	−0.218
(n = 65)	$\bar{N}$	−0.316*	0.179

[a] Standardized to a plot size of 20 ha.
[b] * $P \leq 0.05$; ** $P \leq 0.01$.

Because significant relationships between community stability gradients and habitat type may be masked by considering only the entire sample, we partitioned the analysis by habitat type (Table 9). (Tundra study plots were omitted because of little variation in geographic location.) The significant results are as follows: (1) grasslands: density variation decreases from east to west; (2) scrub forests: species turnover increases from south to north; (3) coniferous forests: species turnover and diversity variation increase from south to north; and (4) mixed deciduous-coniferous forests: species turnover increases from south to north. Overall, even the statistically significant results offer little support for any strong relationship between geographical position and community stability.

Geographical gradients in species richness and abundance.—We examined our data set for geographic gradients in species richness and breeding abundance by computing the correlation between $\bar{S}$ and $\bar{N}$ and latitude and longitude. Over all plots there were three significant correlations (Table 10). The strongest correlation was the negative relationship between $\bar{S}$ and longitude suggesting that mean species richness decreased from east to west. In addition, $\bar{S}$ and $\bar{N}$ generally decreased from south to north. These results generally support the longitudinal relationships reported by Short (1979) but contrast somewhat with his latitu-

TABLE 11. The linear correlation (and partial correlations) of the average proportion of long-distance migrants with each of the stability indices.[a]

	CV(N)	CV(S)	CV(H')	CV(J)	$\overline{T}$	$\overline{CC}$	$\overline{rD}$	$\overline{BC}$	$\overline{P(E)}$
Proportion of long-distance migrants	−0.120 (−0.070)	−0.221** (−0.010)	−0.274** (−0.114)	−0.195* (0.012)	−0.062 (0.049)	0.086 (0.063)	−0.065 (−0.086)	0.018 (−0.133)	−0.023 (0.010)

[a] * $P \leq 0.05$; ** $P \leq 0.01$.

dinal patterns. However, all of these associations are weak, and we are reluctant to make further inferences from these statistics.

We also partitioned the data by habitat type and recomputed the correlations between $\bar{S}$ and $\bar{N}$ and latitude and longitude (Table 10). Only two significant correlations resulted: mean breeding density in coniferous forests and in deciduous forests decreased from south to north. None of the habitat correlations was particularly strong, possibly because $\bar{S}$ and $\bar{N}$ are not monotonically related to either latitude or longitude for most habitat types.

Long-distance migrants as a stabilizing influence.—The habitat types differed extensively in their average proportion of LDM (Table 5; $F_{6,34} = 43.73$, $P < 0.0001$). A posteriori comparisons showed tundra habitats to have a significantly greater proportion than other habitat types, and grassland, scrub, and coniferous forests significantly smaller proportions than mixed deciduous-coniferous and deciduous forests.

The correlations between the proportion of LDM and the stability indices were significant for 3 of the 4 coefficient of variation indices (Table 11). However, for all of the indices the sign of the correlation coefficient suggested that the greater the proportion of LDM among breeding species, the more stable the communities are from year to year. Separate tests of significance of the correlations are not valid because of a high degree of covariation among some of the indices. To address this problem we computed partial correlations, controlling in each case for the linear effects of all the other indices (Table 11). No significant partial correlations were found suggesting a complex relationship among the proportion of LDM and the stability indices. A PCA including the proportion of LDM along with the nine indices showed this variable to load most heavily on the diversity-variation gradient. The sign on the loading suggested that species that are seasonal residents, and migrate long distances to their wintering grounds, may buffer these communities somewhat from extensive annual diversity variation.

DISCUSSION

The overriding impression from our analyses was that few patterns of breeding bird community stability are associated with either habitat or geographical location. We did not expect such an absence of pattern. Published accounts of relationships between geographic location and community stability strongly suggest that northern communities should be less stable than more southern communities (e.g. Fischer 1960; Pianka 1966; Järvinen 1979, 1980). We also were surprised by the lack of correlation between our derived stability gradients and habitat type. From our own experiences with breeding bird communities, primarily in eastern deciduous and coniferous forests, we expected sharp contrasts at least between these habitat types and grassland plots. Overall, our analyses from both habitat and geographical perspectives are most noteworthy for the lack of pattern observed. Our geographical analysis suggested a positive but weak relationship between species turnover rate and latitude. We are uncertain why our results are not in greater accord with those of Järvinen (1979).

Habitat analysis.—In addition to our own research experiences that lead us to suspect differences in stability across habitat types, we cite the obvious contrast between experimental studies of stability following perturbation in eastern forests (Hensley and Cope 1951, Stewart and Aldrich 1951, Noon and Robbins 1983) and recent reports of high annual variability in breeding bird community structure in grassland and shrub-steppe habitats influenced only by climatic variability (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981). Admittedly, the former studies largely document within-season stability. However, in the eastern deciduous forest, stability to a direct perturbation of species populations was apparent both within and across years (Noon and Robbins 1983). This contrast in pattern suggests that the bird communities of these habitat types may actually differ in their stability properties. However, on the basis of a much larger sample, the only significant difference observed between grassland and forested habitats was in relation to annual diversity variation. The relative position of the habitat types along a gradient of diversity variation (factor II; Fig. 2, middle) showed grasslands to be more variable in this dimension.

The only other pattern that we observed was the difference in degree of annual abundance variation among forested habitats. Though not significant, the data suggest that coniferous forests show greater abundance variation than other forest types. Järvinen (1980) reports a similar pattern for northern European bird communities.

What most characterized the ordination of plots by habitat type along the three stability gradients was the extensive variability that occurred within a habitat type. Indeed, with a nonrandom selection of study areas across habitat types, it would be possible to reject almost any hypothesis of no difference in stability. However, with large sample sizes any such conclusions that may arise from smaller-scale analyses quickly disappear. Our results suggest that it is impossible to make general statements such as "grassland breeding bird communities are inherently less stable than those of eastern deciduous forests." Järvinen (1980) also observed that geographic location was of greater importance in determining community stability patterns than habitat.

Given this conclusion, we can suggest explanations for the lack of pattern in community stability across habitat types. One possibility is that much of the variability within a plot is a result of regional changes in land use that affect local populations. This effect may be particularly pronounced in the eastern deciduous forest biome where habitat fragmentation has been severe and apparently has greatly increased avian turnover rates (Lynch and Whitcomb 1977, Whitcomb et al. 1981; but see McCoy 1982). We attempted to minimize such effects by only including plots that have not undergone appreciable habitat change during the period of study. However, it was impossible to control for changes that may have occurred beyond plot boundaries.

Another possibility is that our habitat classifications were too broad, and the heterogeneity that this introduced masked any true habitat differences. However, a compromise was essential when allocating plots to habitat types. Too fine a partitioning would have reduced group sizes, decreased the power of statistical tests, and lowered the precision of estimated mean stability metrics.

The problem of the scale at which stability and its variation have been estimated may contribute to the lack of pattern. Locally derived point estimates of annual stability in community structure may show high variability when compared across plots within a habitat category. This sampling problem arises because we may be attempting to make inferences about community properties based on sampling units too small to reflect the scale at which the processes are occurring (see Wiens 1981, Connell and Sousa 1983).

Total diversity, and its variation, may also be increased by including plots from different geographic regions in a common habitat group. If patterns of variation were generally clouded by collapsing geographically distinct study plots into common habitat groupings, we would expect some of these patterns to reveal themselves in our geographic analyses. However, we found few distinct patterns of geographic variation even when the data were analyzed separately by habitat.

It is perhaps important at this point to recall that the individual plot was the basic unit of our study; each plot carried equal weight in all analyses. As a result, many problems of scale introduced by comparing plots across habitats or biogeographic regions have been avoided. We simply tested whether any patterns emerged as a result of grouping plots on the basis of gross habitat similarity. Our results suggest that individual plots, but not habitat groups, may have distinct patterns of annual variation.

An additional factor contributing to both the observed within-habitat heterogeneity and the few between-habitat differences may be that plots differed in their overall degree of habitat saturation by breeding birds. If certain habitats (or plots) consisted of species populations generally below their carrying capacities, then successive annual censuses from small plots may show extensive variation simply because plot sizes were not large enough to reflect the scale at which population processes acted. To illustrate this line of reasoning we refer to the "checkerboard" model of Wiens (1981). For example, consider a comparison of grassland and deciduous forest plots represented by two checkerboards (habitats) of equal size. We assume that the deciduous forest habitat is considerably more saturated (i.e. has a greater density of territories) than the grassland habitat. Random redistribution of the checkers (territories) on the respective checkerboards would give the appearance of substantially greater density and species variation, relative to plot boundaries, on the grassland plot. This contrast would arise even if the grassland habitat experienced no variation in density or species richness at a regional level. Although this is a very simple model, with several strict assumptions (Wiens 1981), we feel it may accurately portray a difference between those habitat types, or plots, that differ in their degree of saturation by breeding birds.

If Wiens's model is accurate, it suggests that plot size may need to be a function of the degree of saturation in order to make valid between-plot comparisons. However, we feel there is nothing inherently misleading in estimating population processes, and their variability, relative to similar plot sizes. Even if some patterns can be explained by recourse to a simple model of differences in saturation, this does not preclude a role for differences in species or habitat properties. Characteristic undersaturation of some habitats actually may be indicative of underlying biotic and abiotic properties that distinguish them from saturated habitats. Some of these properties may be generalizable across major habitat groupings.

Geographic analysis.—In contrast to much ecological dogma, we did not find strong support for the prediction that northern animal communities are less stable than more southern communities. Factor I, a gradient in species and individual turnover, was significantly correlated with latitude and suggested a positive relationship between latitude and species turnover. Although the overall association between these variables was weak ($r = 0.217$, $P < 0.01$), the relationship between latitude and species turnover became stronger when the data were partitioned by habitat type. Scrub, coniferous, and mixed deciduous-coniferous forests showed particularly strong evidence of decreasing stability with increasing latitude (Table 9), as was found by Järvinen (1979) for Scandinavian forests. Interestingly, deciduous forest plots, our largest sample ($n = 65$), showed no relationship among these variables.

Grassland plots showed a significant decrease in annual abundance variation moving from east to west. This pattern may simply result from the fact that many of the eastern grassland plots were of recent origin and rather small in spatial extent. As a result they were subject to biogeographic influences characteristic of small islands of recent origin (see Whitmore 1980).

Of the five significant latitudinal correlations with the stability gradients, all showed decreasing stability from south to north. Järvinen (1979) examined three hypotheses that attempt to explain similar latitudinal relationships. These hypotheses propose that northern communities are less stable than southern ones because (1) northern communities have lower species richness, (2) northern communities experience greater environmental unpredictability, or (3) environmental productivity decreases northward. Järvinen favored the environmental unpredictability hypothesis.

Our data show a trend of decreasing species richness with increasing latitude, but this pattern is not consistent across habitat types (Table 10). The eastern deciduous forest plots would be particularly confounding in this regard because of the reversed latitudinal gradient in species richness in this biome (Rabenold 1979). To look at the possible influence of species richness on stability we examined the correlation structure between each of the stability gradients and $\bar{S}$. A significant association occurred between the diversity-variation gradient and $\bar{S}$ ($r = -0.528$, $P < 0.001$), suggesting that areas with high $\bar{S}$ values have low diversity variation.

Our study plots could be ordinated along an environmental predictability gradient (separately for variables such as temperature and rainfall), but we doubt if this gradient would clearly parallel a gradient in either latitude or longitude. In general, we expect northern bird communities to be exposed to greater environmental variability at a given longitude, but when considering longitude and latitude together such patterns are easily obscured (see Rotenberry 1978). Length of the breeding season, probability that the breeding season will be disrupted by climatic events, and the probability that such climatic events would surpass a bird's physiological thresholds all increase with increasing latitude. However, we do not believe that any of these factors would increase monotonically with latitude for the study areas in our data set.

The magnitude of seasonal fluctuations in resource productivity also varies positively with latitude (Ricklefs 1980). However, it is difficult to imagine distinct monotonic gradients in productivity paralleling latitude for the same reasons that confound the geographic relations of climatic predictability. In general, extensive seasonal variation in productivity would decrease species diversity (MacArthur 1972), and presumably stability, by increasing the probability of extinction among small populations.

However, we feel we cannot easily relate trends we observed to productivity differences because of the suspected importance of annual variability at the local level. Local-level effects could easily be of different magnitude, or sign, from regional trends in productivity.

The weakness of the relationship between latitude and stability may have been a consequence of the length of our latitudinal gradient. Although our sample plots covered more than 40° in latitude, we had no samples from subtropical or tropical communities. It may well be that the functional relationship between latitude and stability does not show a smooth decline with decreasing latitude, but rather changes abruptly when one moves from temperate to tropical regions.

In summary, we are reluctant to draw conclusions about geographical gradients in stability because the relationships that we observe are not very strong and are not consistent across habitat types, and because it is difficult to infer any causal mechanism for the patterns that we do observe. Patterns are confounded by covariation in latitudinal and longitudinal influences, as well as possible local effects. The reader is referred to Järvinen (1979) for a discussion of the way in which similar correlational results have been interpreted.

Long-distance migrants as a stabilizing influence.—If we assume that breeding abundance is positively related to saturation, our data suggest a weak association between this variable and the proportion of LDM ($r = 0.147$, $0.05 < P < 0.10$). However, this relationship is confounded by geographic effects ($r_{\text{LDM,lat.}} = 0.442$, $P < 0.001$). Controlling for the linear effects of latitude and longitude by partial correlation analysis showed the correlation between the proportion of LDM and $\bar{N}$ to be even stronger ($r = 0.313$, $P < 0.001$). That is, there is a tendency for communities with higher abundances to have a larger proportion of LDM, with this relationship dependent on geographic location.

The possible stabilizing influence of a large proportion of LDM (Table 11) may be a function of its correlation with $\bar{N}$. If excess birds are excluded from breeding in saturated communities, they may act as a buffer to within-season perturbations. As a result, these communities would give the appearance of a more stable annual pattern. As a corollary, communities close to saturation may be more likely to produce an excess of individuals and thereby maintain stability by increased recruitment. Collectively, these correlations suggest that northern communities may be characterized by even greater instability were it not for the stabilizing influence of a large, annual influx of LDM.

Patterns of variation in community stability.—Despite the lack of pattern in our derived gradients, our analyses did reveal three apparently independent sources of variation in community predictability. Breeding bird communities can independently show annual variation in species composition, species richness and equitability, and breeding abundance. Individual communities may be subject to one or any combination of these three sources of variation. We have illustrated that there is little tendency for any of these sources of variation to be closely associated with either gross habitat structure or geographic location. However, we are struck by the clarity of these synthetic gradients and believe that they have increased our understanding of the manner in which avian communities may vary from year to year.

Our results also suggest a positive relationship between community stability and both average species richness and breeding density. Järvinen (1980) reported a similar pattern for Scandinavian bird communities. Communities with higher values for $\bar{S}$ and $\bar{N}$ tended to be more stable, a pattern that was reflected in all nine of our indices (Table 2). Admittedly, $\bar{S}$ is a function of plot size up to some asymptotic limit that may vary by habitat type (James and Rathbun 1981). However, to a large extent we controlled for this source of variation by excluding from our analyses plots <9 ha in size. Across-habitat comparisons may still have been confounded by a possible residual relationship between area and $\bar{S}$.

To rigorously test for differences in $\bar{S}$ by habitat, differences in plot size, or abundance, could be normalized by the method of rarefaction (see Simberloff 1978, James and Rathbun 1981). This is a separate question that we are considering elsewhere (Noon and Kelly in prep.). However, we believe that our current estimates accurately reflect the true rankings of habitats by species-richness values. We have little evidence that plot size affected our estimates of $\bar{S}$, as the correlation between these two variables over all the data was nonsignificant ($r = 0.049$, $P \gg 0.05$). Even when the data were partitioned by habitat only two significant correlations resulted, and these were small and of opposite sign.

There is a strong inverse relationship between $\bar{S}$ and the coefficient of variation indices. However, speculation about the significance of the relationship to the diversity-stability controversy seems injudicious at this time. Our findings do suggest that diverse, high-density communities are more stable than less diverse, low-density systems (Table 2). The relative contributions of species richness and breeding abundance to stability is unclear; in addition, these variables are highly correlated ($r = 0.449$). The coefficients of variation indices showed stronger linear relationships with $\bar{S}$, and the remaining indices were more strongly associated with $\bar{N}$ (Table 2). Partial correlation analysis, controlling for the confounding effects of either $\bar{S}$ or $\bar{N}$, verified these patterns. Thus, the relative influence of species richness or abundance is dependent upon which indices are used to measure stability.

McNaughton (1978) observed similar species-richness differences in plant communities of African grasslands and attributed much of the enhanced stability of diverse systems to the arrangement of these communities into guilds (see King and Pimm 1983 for an alternative explanation). As communities become more species-rich, guild structure becomes more pronounced, and the average overall interaction strength among species declines (McNaughton 1978, Colwell 1979). There are extensive biotic interactions within a guild and very little interaction across guilds. The decreased average connectance among the species composing the community could enhance the stability properties of the system (May 1972).

Guild structure was excluded from our analyses, but many avian guild studies suggest that bird communities are organized in this manner (e.g. Cody 1974, Willson 1974, Holmes et al. 1979, Landres and MacMahon 1980, Short and Burnham 1982, Verner 1984). A direct relationship is expected between the number of guilds (defined at a given similarity level) and the bird species richness of the community. If a guild substructure in a species-rich community produces stability through a lowering of average species connectance, it provides a partial explanation for the results we observed.

Future efforts to understand patterns in community stability.—There are several additional sources of information on avian populations that, if more generally available, would give insight into the causes of variability in community stability. For example, many of the contrasts in stability patterns that we observed are explained by a simple model of differences in saturation of the available habitat by breeding birds. Related to this possible influence is the observation that there are few studies that document the number and sex ratio of nonbreeding individuals (= floaters) in these habitats. Clearly, a supply of nonbreeding but physiologically capable and motivated individuals could act as a buffer to within-season perturbation to the breeding component and add to the observed stability of a community.

Community stability, at least as estimated by many of the metrics used in this study, would be enhanced if populations experienced compensating fluctuations in abundance. Compensatory shifts would suggest nonindependence of the species populations. A method of detecting and testing for significant covariation patterns has recently been proposed by Schluter (1984), and we are in the early stages of examining this data set for the prevalence of such patterns using his method.

Within any one habitat type we generally observed extensive variation in stability properties. It would be of interest to contrast, in more detail, those communities that are either particularly stable or unstable, while controlling for the confounding effects of gross differences in habitat structure. Such contrasts may go a long way toward revealing the processes underlying different patterns of annual variation.

As a final recommendation, several recent studies (Grossman 1982, Grossman et al. 1982, Connell and Sousa 1983) have indicated that the accuracy of stability estimates are improved if the study period covers at least one complete turnover (2–3 average lifespans) of all individuals in the community. Many of our shorter time-series studies did not meet this standard. In this regard, it would be of interest to recalculate our stability estimates in 5–10 yr when more long-term census data are available and determine if our current conclusions need to be amended.

ACKNOWLEDGMENTS

We thank Edward Connor, Michael Morrison, Ronald Mumme, James Nichols, Olli Järvinen, and

Jared Verner for reviewing the manuscript and offering many helpful suggestions.

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A PHENETIC ANALYSIS OF THE REDPOLLS *CARDUELIS FLAMMEA FLAMMEA* AND *C. HORNEMANNI EXILIPES*

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ABSTRACT.—A review of the historical treatment of Common and Hoary redpolls (*Carduelis flammea flammea* and *C. hornemanni exilipes*) revealed no diagnostic means of distinguishing the two taxa. Interpretations of species limits have varied, resulting in conflicting treatment of intermediate forms. Variability in plumage and skeletal characters of redpolls from 9 breeding locations in Alaska and Canada were examined to determine if a means of discriminating between the two taxa could be found, and to determine if individuals with intermediate plumage characteristics (potential hybrids) were also morphologically intermediate. Because sexes differed in most skeletal dimensions, all analyses were duplicated for the two sexes. A character index was developed based on three plumage characteristics: rump streaking, undertail covert streaking, and lateral (side) streaking. This index characterized redpolls on a darkness gradient from extreme *flammea* (dark, heavy streaking) to extreme *exilipes* (light, no streaking). The observed range of scores was divided into thirds to designate *flammea*, unknown (intermediate), and *exilipes* classes. Females showed a much narrower range of plumage variability than males. No females were white enough to be considered *exilipes* on the scale used for males. Most birds from the *flammea* and *exilipes* extremes of plumage variability could be distinguished by skeletal criteria (using discriminant function analysis); however, no discontinuity existed, as other birds were intermediate for both plumage and skeletal characteristics. Intermediates were found at all sampled localities where both plumage morphs occurred. Results of analyses based on plumage (character index) and skeletal measurements were very similar and showed that samples containing intermediate plumage birds were also intermediate skeletally. Considering the continuous variability of both plumage and skeletal characters and the lack of any diagnostic criterion for identifying the taxa, the two redpolls should be merged into a single taxon, *Carduelis flammea*. *Received 22 November 1983, accepted 23 May 1984.*

COMMON and Hoary redpolls (*Carduelis flammea* and *C. hornemanni*) are small finches of the subgenus *Acanthis* (A.O.U. 1983). The taxonomy of redpolls has long been perplexing. Jehl and Smith (1970) considered it to be "one of the most perplexing problems in North American ornithology." Similar concerns were expressed by Bannerman (1953), Todd (1963), and others. Coues (1862) recognized 6 species of redpolls in North America, plus another in Europe; Salomonsen (1950) listed only one worldwide, while the American Ornithologists' Union (1983) recognized two. Of the many problems in our understanding of the relations of the various redpoll taxa, the specific distinction of *C. flammea* and *C. hornemanni* is of primary importance. The relationship of the most widespread subspecies of each of these species, *C. f. flammea* and *C. hornemanni exilipes*, is central to this problem.

This study was an attempt to clarify the relationship between these two redpoll taxa using plumage and skeletal characters. Alaska redpolls were considered in detail because published accounts indicate that the greatest taxonomic difficulty in North America occurs in this region (Gabrielson and Lincoln 1959, Baldwin 1961). Smaller samples from across Canada also were analyzed.

Characteristics previously used to distinguish *exilipes* from *flammea* are listed in Table 1. No single character distinguishes these taxa from each other unequivocally. The generalizations that exist are useful for identification of extreme examples only. Unfortunately, no description of the range of variability in either *exilipes* or *flammea* has been made, resulting in

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TABLE 1. Differences in bill and plumage characteristics used to distinguish between *Carduelis hornemanni exilipes* and *C. flammea flammea*.

Character	*exilipes*	*flammea*	Source
Bill length	Small	Moderate	Coues 1903
Bill shape	More conic, less compressed, darker colored with dense nasal plumuli	Opposite	Coues 1862
Superciliary stripe	More distinct	Less distinct	Coues 1862
Breast color	Rosy, many shades lighter than *flammea*	Darker	Coues 1862
Sides	Paucity of streaks		Coues 1862
		Strongly streaked flanks	Bannerman 1953
Feet	Smaller, weaker Toes much shorter	Opposite	Coues 1862
	Tarsus > middle toe plus claw	Tarsus = middle toe plus claw	
General	Lighter	Much darker	Godfrey 1966

confusion as to how to identify specimens that are apparently intermediate in some characters.

Because they were originally described using morphological criteria, any attempt to determine whether *flammea* and *exilipes* are indeed separate species logically should look for at least one morphological feature to discriminate between them. If a character can be found with a range of states such that the distribution of scores of samples of the pure species is discontinuous (the discontinuity indicating species limits), suspected hybrids should have intermediate scores along this character.

Under the strictest definition of the biological species (Mayr 1970), the presence of any hybrids would make the specific distinction of the parental taxa suspect. However, it has been common practice to accept species distinctiveness if hybridization is limited. Hence, if few intermediates exist, whether they be hybrids or extreme variants of parental species, the separation of *exilipes* and *flammea* would be justified. For the purpose of this paper, both hybrid and intermediate are used to describe birds that possess characteristics intermediate between "typical" *flammea* and *exilipes*. If these two forms are morphologically distinct, then intermediates are probably true hybrids or their offspring. If *flammea* and *exilipes* are not distinct, the intermediate birds probably represent a segment of continuous variation rather than hybrids, and it is necessary to conclude that the recognition of two species is unfounded.

Two methods often used to detect the presence of hybrid individuals and/or populations are hybrid indices (examples using avian subjects include Sibley and Short 1959a, b; Sibley and West 1959; Short 1963; Szijj 1963; Rising 1970; and Scott et al. 1976) and multivariate analyses of skeletal dimensions (Rohwer 1972). Although frequently used to identify hybrids (or populations containing hybrids), hybrid indices do not directly reflect the hybrid nature of the individual to be scored. I have used the term "character index" because the scale is derived from several characters. Plumage characters used in character indices are often the same variables that give rise to the hypothesis of hybridization in the first place, and their use can lead to a circular argument (Scheuler and Rising 1976). I used the analysis of skeletal characters as an independent test of the findings of the character index analysis.

METHODS AND MATERIALS

Specimens.—Only adults collected during the breeding season were used in the plumage and skeletal studies. Alaska redpolls were collected in three regions: the Akulik-Inglutalik River delta, Norton Bay; Interior Alaska (no large collections were made, so this sample comprises three smaller samples: Talkeetna Mountains near Hatcher Pass, Denali Highway at the Brushkana River, and Fairbanks); and the Kongakut River, Arctic National Wildlife Refuge. Four redpolls collected at Kaktovik, Barter Island, were added to the Kongakut River sample. These speci-

Table 2. Number and location of specimens from which skeletal measurements were taken.

Location	Males	Females
Akulik-Inglutalik River delta, Alaska	100	51
Interior Alaska	21	11
Kongakut River, Alaska	67	31
Inuvik, N.W.T.	38	18
Krekovick Landing, N.W.T.	17	10
Coppermine, N.W.T.	16	11
Churchill, Manitoba	8	—
Winisk, Ontario	8	—
Fort Chimo, Quebec	37	8
Total	312	140

mens have been deposited in the collections of the American Museum of Natural History and Royal Ontario Museum. Samples from localities across Canada were measured at the Royal Ontario Museum. Canadian collection sites were Inuvik, Northwest Territories (N.W.T.); Krekovick Landing, Anderson River, N.W.T.; Coppermine, N.W.T.; Churchill, Manitoba; Winisk, Ontario; and Fort Chimo, Ungava Bay, Quebec. Numbers of specimens from each collection site are listed in Table 2. The location of each collection site is shown in Fig. 1.

Redpolls used in the following analyses were prepared as partial skins and skeletons, providing plumage and skeletal data from each specimen.

CHARACTER SELECTION

Skeletal characters.—A list of skeletal characters that have been used in avian morphological studies was compiled from the literature (Johnston 1969; Schnell 1970; Power 1971a, b; Robins and Schnell 1971; Johnston and Selander 1972; Rohwer 1972; Rising 1973). I selected 38 variables from the list as being of possible value in this study. The 38 variables were measured with dial calipers to the nearest 0.1 mm on a sample of 70 birds constituting the most extreme examples (based on rump color) of female *flammea* (n = 25), male *flammea* (n = 20), and male *exilipes* (n = 23) in my Alaska collections. Only 2 female redpolls with white rumps were found; hence female *exilipes* were not treated as a group in the preliminary analyses.

I tested the three groups using discriminant function analysis (DFA) to determine the value of skeletal characters in discriminating species. I also examined differences in the means of each variable between pairs of the three samples using t-tests, and omitted variables that were not significantly different between at least one pair of my reference groups. By these methods I reduced the character set to 19 variables that could be measured with good repeatability and would be useful in discriminating between morphs of redpolls (see Table 3).

An attempt was made to measure the length of the middle toe, as this was an important character in the description of *exilipes* by Coues (1862). Unfortunately, this character proved to be difficult to measure due to the problem of uniformly straightening the toe of dried specimens. Since Coues (1862) stated that all toes are short in *exilipes*, the hallux measurement should have provided an index of this characteristic. The hallux is a single bone and as such is more easily (and precisely) measured than the middle toe, which comprises three elements. Because I measured the hallux on skeletons, its length does not include the claw.

Plumage characters.—Several plumage characters may differ between *flammea* and *exilipes* (Table 1). Some differences are subtle, particularly during the breeding season when the feathers have become worn. In order to place birds on a gradient between the two species, it was desirable to have characters that showed a broad range of variability so that several classes could be established. Three characters were selected as having sufficient variability to be useful: 1) rump streaking, 2) undertail covert streaking, and 3) streaking on the sides and flanks.

For each of the three plumage characters scored, reference series were established showing the gradation from Common to Hoary plumage states. Six classes were used for each character, giving each variable equal weighting in the character index. The range of variability of these characters is shown in Figs. 2-4.

ANALYSES

Missing data estimation.—The use of multivariate statistical techniques such as DFA requires that no missing values exist in the case (individual) × variable data matrix. Unfortunately, skeletal characters occasionally were impossible to measure due to breakage (particularly if specimens were collected by shooting) or loss. Since a given specimen had few (if any) missing characters, I felt it was more desirable to include the specimen in the analysis than to omit it altogether. Missing values were estimated using regression equations of the character with the missing value and the character most correlated with it. Regressions were calculated for each sex and location, provided a sufficient number of individuals (15-20) were available. Approximately 1-2% of the measurements were estimated.

Sexual dimorphism.—The samples used in this study were tested for sexual dimorphism using the skeletal data set. These data were subjected to DFA (BMDP7M, Dixon 1975) for all locations pooled. Most studies using morphological data have included separate analyses for the sexes, but rarely have the differences between the sexes been specifically analyzed (see Johnston 1969). In evaluating the success of this and other discriminant functions (see *Skeletal analysis*) the

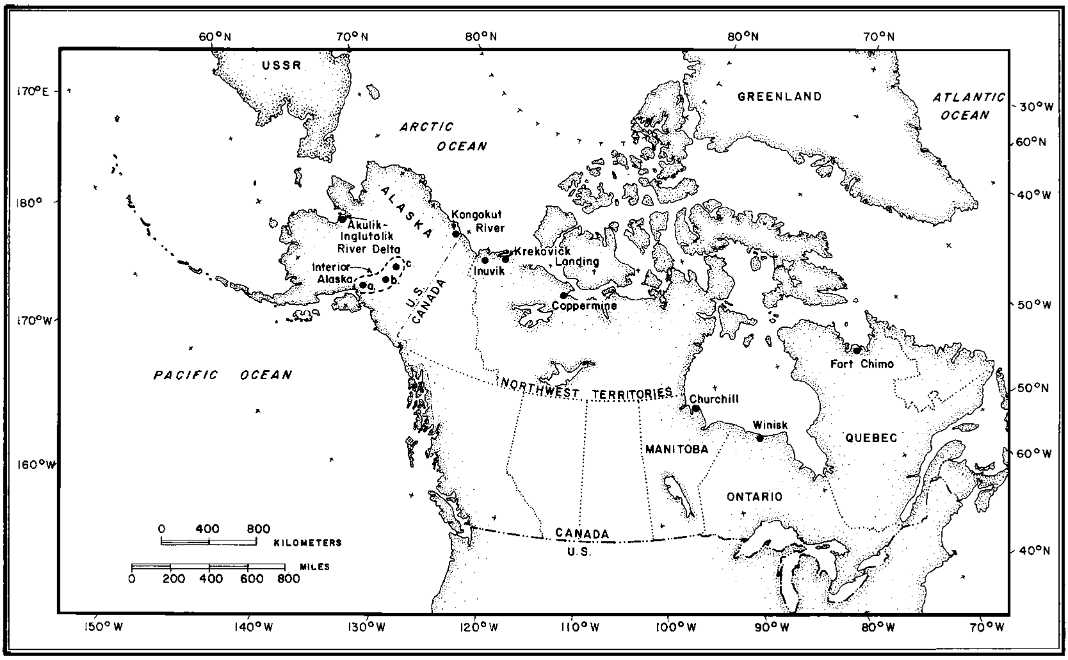

Fig. 1. Locations of collection sites of redpolls. Subsamples from Interior Alaska are: a) Hatcher Pass, b) Brushkana River, and c) Fairbanks.

jackknife method was used to determine the percentage of specimens that could be correctly classified.

Hybridization.—The ideal analysis of hybridization involves the collection of samples of each parental species (from areas of allopatry) and then of the putative hybrid population at an intermediate location. The difficulty in using this method with redpolls was in finding a region where only *exilipes* occurred. Several maps, such as those published in Dement'ev et al. (1954) and Ogilvie (1976), show a northern band where only this form occurs. This band is particularly broad in the Keewatin District, N.W.T. However, regional works such as Snyder (1957) and my own observations in western and northern Alaska and Keewatin District, N.W.T., indicate that both forms are sympatric in these areas as well. Wynne-Edwards (1952) wrote that the northern limit of *flammea* is roughly coincident with the northern limit of *hornemanni*. Thus, pure populations of *exilipes* may not exist, and it was necessary to select the reference series of the parental forms from the same samples as those containing the presumed hybrids. This method reduced the compounding effects of geographic variation since the entire analysis was done by location; however, a more precise means of delimiting the parental species had to be used.

Character index analysis.—One method of measuring the extent of hybridization in natural populations is the formulation of character (=hybrid) indices. To use this method, several characteristics that differ between the species are selected and a graded series is developed over the range of variability. A character index was computed for redpolls using the formula:

$$\text{character score} = \text{rump score} + \text{undertail covert score} + \text{lateral streaking score} - 2.$$

This scoring system resulted in each bird being placed along a gradient between 1 (extreme *flammea*) and 16 (extreme *exilipes*). The distribution of scores reveals the presence of intermediate (hybrid) birds. When examined by location, the scores indicate 1) where intermediates occur, 2) if both parental types are present, and 3) if variation is within or between populations.

Skeletal analysis.—For the purpose of this analysis, individuals were classed as *flammea*, unknown, or *exilipes* by dividing the range of character index scores into thirds. Females exhibited a narrower range of plumage variability than males; hence, a different classification scheme had to be used for each sex. For males, individuals with scores 1-5 were considered *flammea*, 6-11 were unknown, and 12-16 were *exilipes*. For females, individuals with scores 1-4 were considered *flammea*, 5-8 were unknowns, and 9-11

TABLE 3. Mean values (mm) of skeletal measurements of *exilipes* and *flammea*. Taxa are defined as for the discriminant function analyses. Pairs of values marked with an asterisk (*) are significantly different ($P < 0.05$). Significant differences between the sexes are not shown.

	Males			Females		
	exilipes		*flammea*	*exilipes*		*flammea*
Premaxilla length	7.73		8.09	7.49	*	8.03
Premaxilla width	4.59	*	4.51	4.49		4.49
Dentary symphysis length	4.52	*	4.88	4.32	*	4.90
Mandible width	11.79	*	11.47	11.58	*	11.36
Coracoid length	14.48	*	14.62	14.06	*	14.29
Scapula width	2.55		2.58	2.43	*	2.55
Furcula length	13.62		13.66	13.30	*	13.55
Tibiotarsus length	22.28		22.28	21.98		22.00
Tibiotarsus width	1.97	*	2.22	1.94	*	1.98
Tarsometatarsus length	14.18	*	14.35	13.96		14.00
Femur width	2.36		2.37	2.37	*	2.35
Hallux length	4.27	*	4.80	4.21	*	4.75
Humerus length	13.54		13.57	13.13		13.24
Ulna length	16.72	*	16.97	16.03	*	16.35
Radius length	14.91	*	15.14	14.24	*	14.51
Sternum length	17.07	*	17.30	16.32	*	16.71
Keel length	14.39	*	14.92	13.39	*	14.14
Keel depth	6.43	*	6.65	6.13	*	6.38
Synsacrum width	10.60	*	10.34	10.49	*	10.14

were *exilipes*. The *exilipes* and *flammea* classes included only extreme-plumaged birds; therefore if there are indeed two distinct taxa of redpolls, their classes almost assuredly would be "pure." Because I have no evidence that, for example, 5 is a better demarcation for *flammea* than is 6, the unknown samples may have included some *exilipes* and *flammea* as well as intermediates. These groups were then subjected to a DFA. The unknown group was not used in the calculation of the discriminant function, but individuals in this group were scored along it. If the intermediately plumaged birds included hybrids, it was predicted that some would have skeletal dimensions intermediate between those described for *flammea* and those for *exilipes*.

RESULTS

Sexual dimorphism.—Male and female redpolls had different dimensions for several skeletal elements. Using DFA, 89.0% of the pooled (all locations) sample could be sexed correctly using dimensions of skeletal characters (Fig. 5). The between-group difference was highly significant ($F_{7,447} = 77.18$, $P < 0.001$).

The important variables used for discriminating between sexes were radius length, tibiotarsus length, hallux length, keel length, ulna length, keel depth, and mandible width. The magnitude of the differences between sexes for these and other skeletal measurements can be seen in Table 3.

CHARACTER INDEX SCORE ANALYSES

Figure 6 shows the distribution of character index scores for all individuals. Females were much less variable than males. Because the character states were defined independently of sex, the lower variability of females was a property of the birds rather than of the scale used. The three plumage variables used were those that had the greatest range of variability in females as well as in males, although the range was slightly less for females. (In my samples the maximum score for rump and lateral streaking in females was 5; all classes of undertail coverts were found.) Both sexes had continuous distributions of scores.

Males.—The distributions of scores were analyzed by locality (Fig. 7). The three Alaska locations had very different proportions of the redpoll phenotypes. Interior Alaska redpolls were only of the *flammea* type. Both of the remaining locations had a broad range of plumage variants; however, the redpolls of the Akulik-Inglutalik River delta were distributed rather evenly across all classes, whereas the distribution of scores from the Kongakut River

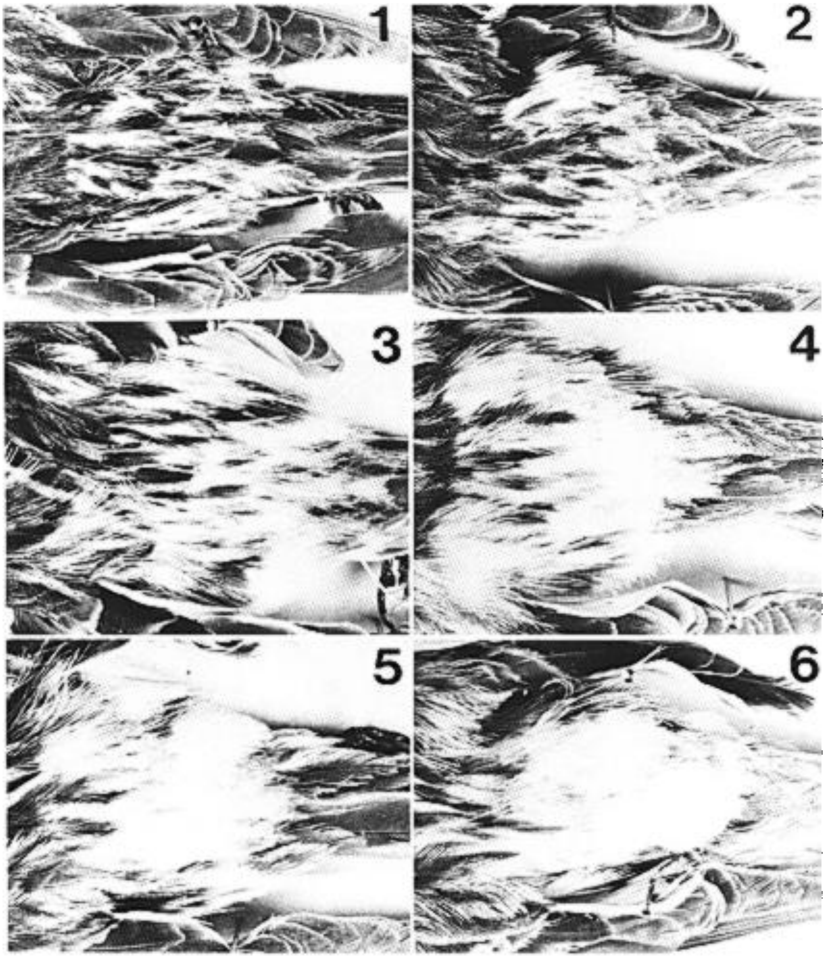

Fig. 2. Character states for the plumage character "rump."

site was skewed toward the *exilipes* type. Since both the Akulik-Inglutalik River delta and the Kongakut River locations had both phenotypic extremes but no evidence of bimodality in the distributions, it appears that interbreeding occurs freely where both alleged species occur together. Both Krekovick Landing and Coppermine had predominantly *exilipes*-like birds but with several intermediates. The remaining locations (Inuvik, Churchill, Winisk, and Fort Chimo) had distributions weighted to the *flammea* end of variability but with intermediates (and occasionally *exilipes*, as at Inuvik) also present.

For males, southern locations tended to have only redpolls of the *flammea* type; *exilipes* predominated in the north but not in pure populations. If only one extreme was present, the distribution was usually skewed, indicating that intermediates were present. Nowhere were both forms present without intermediates.

Females.—The results of the analysis of females were similar to those for males. The distributions of scores are shown in Fig. 8. The Interior Alaska sample contained only birds from the *flammea* range of variability. The Akulik-Inglutalik River delta and Kongakut River samples both included a broad range of morphs. Of the remaining samples, Krekovick Landing and Coppermine both had mostly *exilipes*-like birds but also some intermediates. Inuvik was the reverse, with primarily *flammea* tendencies.

As with males, the female samples provided little evidence for the recognition of two dis-

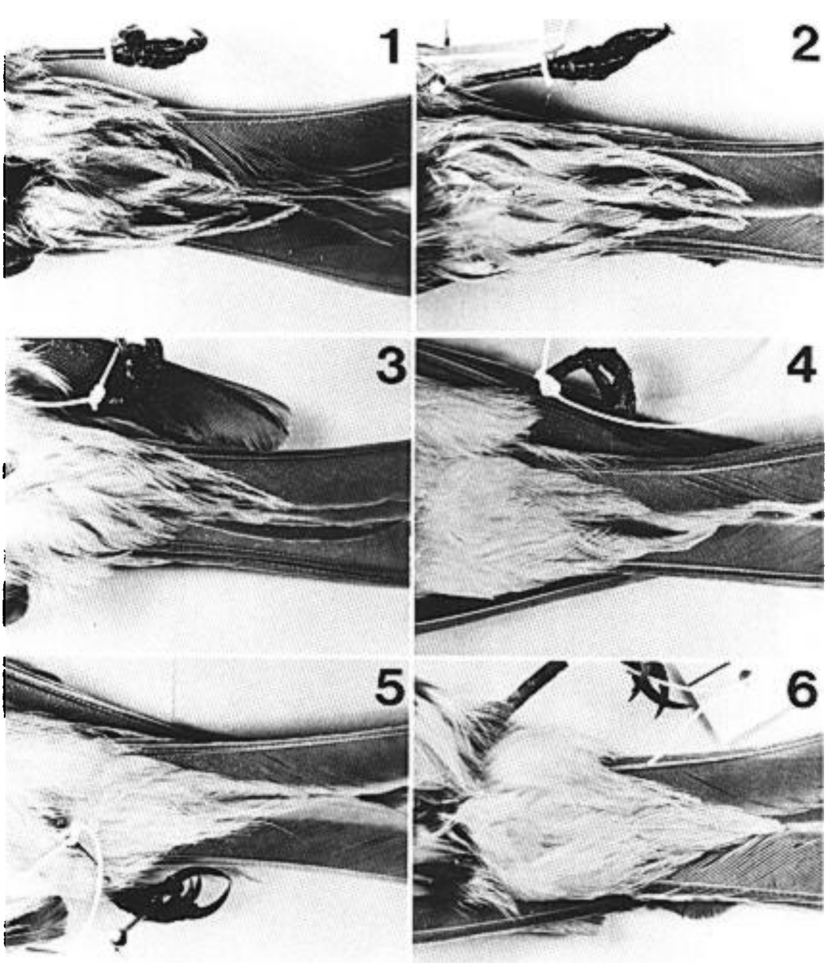

Fig. 3. Character states for the plumage character "undertail coverts."

tinct species of redpolls. Either a continuum of plumage types or only one extreme was present at each locality.

DISCRIMINANT ANALYSES

Both males and females had continuous score distributions (Fig. 9). The absence of a gap between the distributions of the reference samples makes the detection of morphologically intermediate specimens impossible. References to intermediates in the remainder of this analysis indicate that, for the sample under consideration, a greater proportion of birds had scores in the intermediate zone (close to -1) than occurred in the analysis using only "pure" *flammea* and *exilipes*.

Males.—Figure 10 shows the distribution of scores for the *exilipes, flammea,* and unknown samples as defined by character index scores. The two reference samples (extremes) could be separated with a high degree of confidence (96.1% correctly classified) based on skeletal measurements. The difference between these two groups was highly significant ($F_{5,147} = 72.40$, $P < 0.001$). The variables used to maximize the differences between the two reference samples were hallux length, mandible width, premaxillary length, tarsometatarsus length, and keel length.

The sample of unknowns was different from either reference sample in that it had a broad distribution of DFA scores and was somewhat bimodal. However, this sample contained many

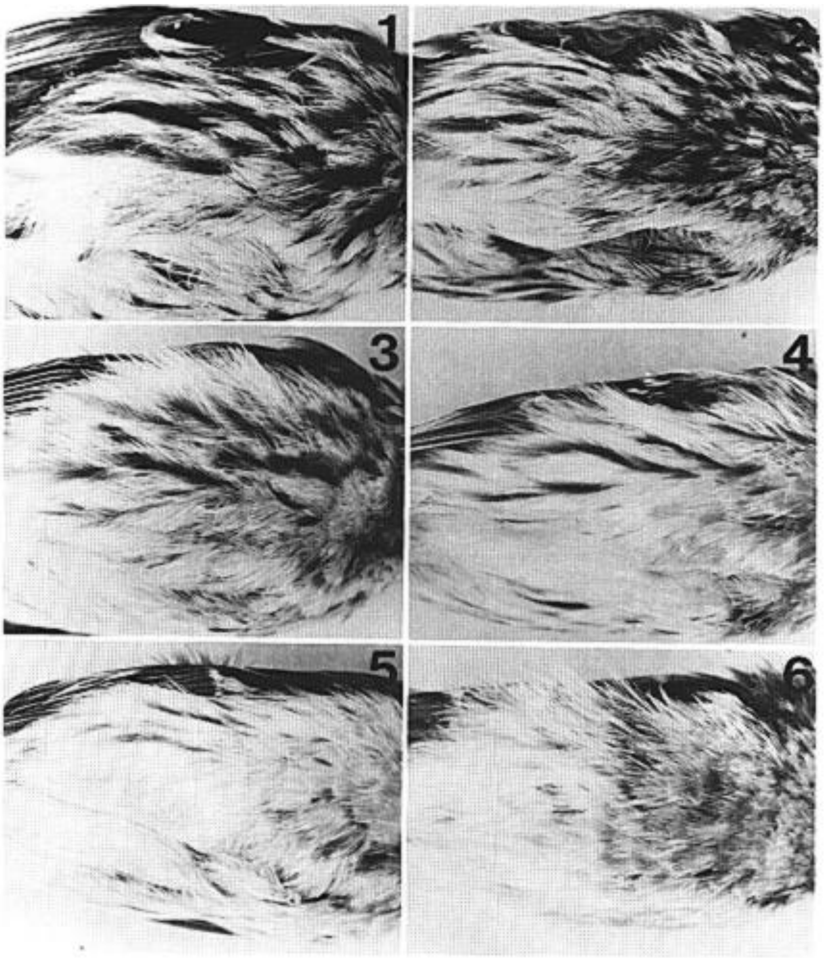

Fig. 4. Character states for the plumage character "lateral streaking."

more birds with intermediate (close to −1) scores than did the reference samples, as was predicted for a sample that contained hybrid birds.

When examined by location (Fig. 7), the results were similar to those from character index scores. The Interior Alaska sample was restricted (with one exception) to the *flammea* range of the distribution. The Akulik-Inglutalik River delta sample was variable, with all types fairly evenly represented. Great variability also occurred in the Kongakut River sample; however, this sample had a skewed distribution with *exilipes*-type predominating. Both the Krekovick Landing and Coppermine samples were predominantly *exilipes* but included some intermediate and *flammea*-like specimens. Inuvik redpolls were predominantly *flammea*-like, but a few birds were skeletally intermediate or like *exilipes*. The remaining samples from Churchill, Winisk, and Fort Chimo were almost exclusively in the *flammea* range.

Females.—The results of the DFA of female redpolls are illustrated in Fig. 10. Although the distributions of scores of the *exilipes* and *flammea* classes showed no overlap, the more conservative jackknifed classification analysis resulted in 94.3% correct identification, thus indicating some potential overlap. The two groups were significantly different in skeletal characteristics ($F_{3,661} = 69.36$, $P < 0.001$). The variables used in the discrimination were hallux length, premaxillary length, and synsacrum width.

When females of intermediate plumages were classified using the same function, the scores

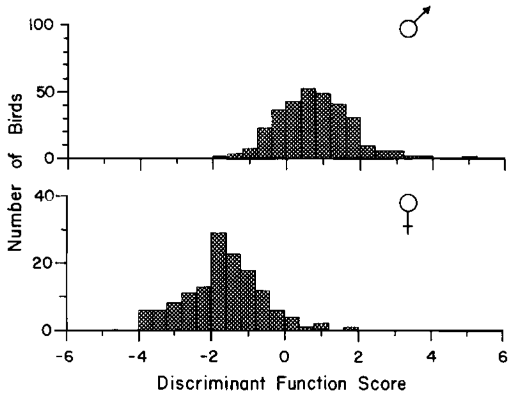

Fig. 5. Distribution of scores of male and female redpolls along the discriminant axis maximizing the differences between sexes (all locations pooled).

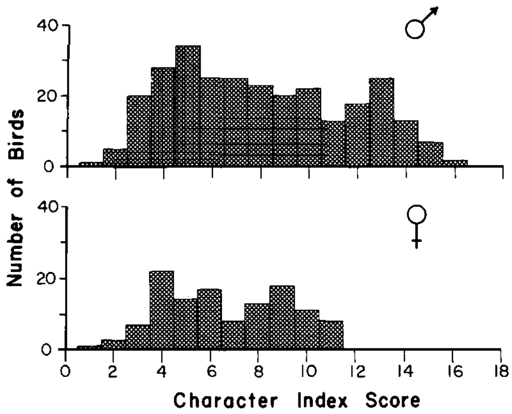

Fig. 6. Frequency distributions of character index scores (all locations pooled) for male and female redpolls.

encompassed the same entire range of variability (2 birds had even higher scores than birds considered to be *exilipes* by plumage). As with males, many more birds were skeletally intermediate in the unknown sample than in either the *exilipes* or *flammea* samples.

When each location was considered individually (Fig. 8) the results were similar to those found for males. All individuals from Interior Alaska had scores in the *flammea* range of variability. Both the Akulik-Inglutalik River delta and the Kongakut River samples exhibited almost continuous variation. The Kongakut River sample distribution was skewed with many *exilipes*, fewer intermediates, and still fewer *flammea*-type redpolls. All of the Krekovick Landing individuals had scores in the *exilipes* range. The Coppermine sample was predominantly *exilipes*, but the extreme of variability extended into the *flammea* range. The Inuvik sample was predominantly *flammea*-type, but there were a few birds in the *exilipes* range of scores.

Overall, skeletal variability in female redpolls appeared similar to that of males. At some locations birds were predominantly of one form (e.g. *flammea* in Interior Alaska, *exilipes* at Krekovick Landing), but wherever both extremes were present, there was no evidence of bimodality in the distributions. It thus appears that wherever the two redpolls are sympatric, they behave as a single species.

DISCUSSION

The analyses show that at some Alaska locations the entire range of plumage and skeletal variability exists. Although the groups that I defined as *flammea* and *exilipes* by plumage characters could be separated using skeletal measurements with a high level of accuracy, the difference was small and there was no discontinuity in variation between the groups. Since the "unknown" groups (intermediate plumage characteristics) were also intermediate between the two "pure species" with respect to skeletal characters, the hypothesis that they included hybrids is supported. This conclusion is strengthened by the fact that similar results were obtained for interlocality and intralocality comparisons, regardless of sex or character set examined.

Canadian samples provided supportive results. Although none of the samples examined contained the entire range of variability, most had skewed distributions, including phenotypically intermediate birds. Samples that contained both *flammea* and *exilipes* always contained intermediates as well.

The absence of a discontinuity between the distributions of the *flammea* and *exilipes* reference samples in the DFA results hindered the detection of hybrids, thus making statements about individual birds impossible. The lack of a discontinuity in itself indicates that there is little morphological difference between these taxa. Rohwer (1972) found much larger differences between the two similar-appearing meadowlarks, *Sturnella magna* and *S. neglecta*. The meadowlarks could be separated using principal component analysis, thus demonstrating that the major trends in variation reflected species differences.

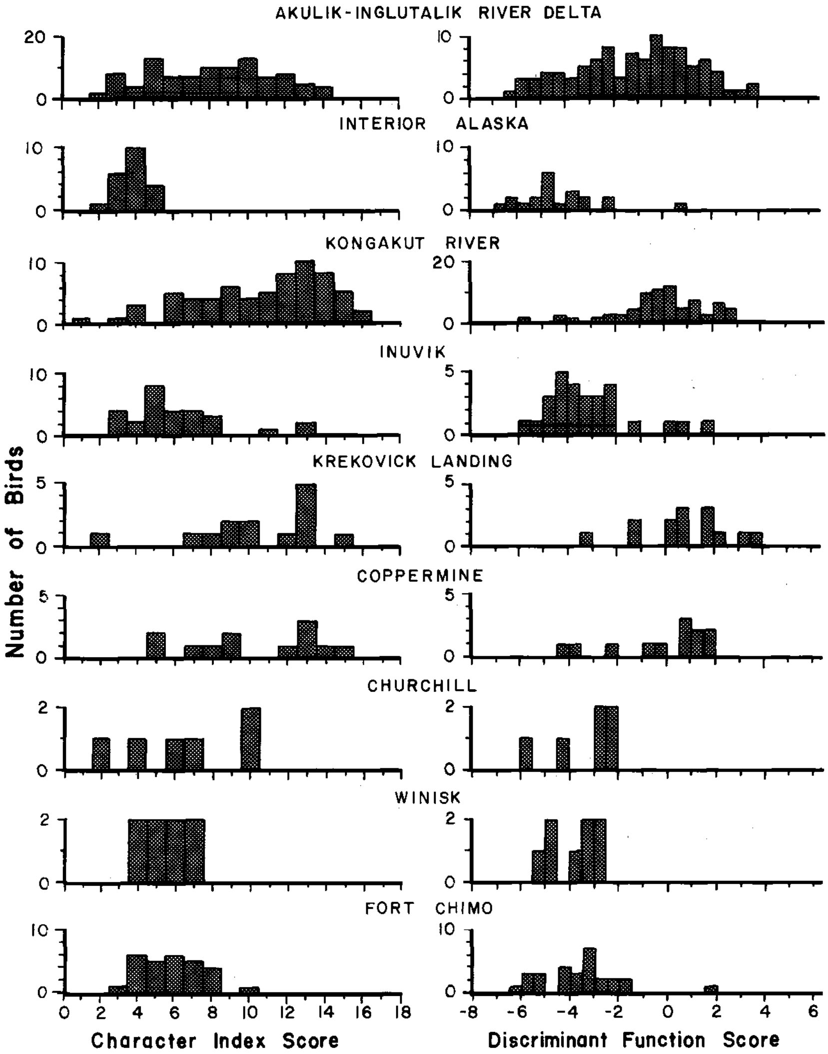

Fig. 7. Frequency distributions of character index and discriminant function scores of male redpolls.

Although there were both plumage and skeletal differences between extreme *flammea* and *exilipes*, the morphological differentiation was slight. Both skeletal and plumage characters show continuous variation. It is necessary to conclude that any distinction between *flammea* and *exilipes* is an arbitrary one. This conclusion is in agreement with the views of authors from other portions of the redpoll's range, in particular those of Salomonsen (1950) in Greenland, Williamson (1961) and Harris et al. (1965) in northern Europe, and Dement'ev et al. (1954) in the Soviet Union.

There are some published opinions in disagreement with my findings that need to be addressed. These opinions relate to the subject of assortative mating and of the morphs found at some of my sample locations.

Positive assortative mating of redpolls was reported by Jehl and Smith (1970) at Churchill and by Wynne-Edwards (1952) on Baffin Island. The possibility of assortative mating poses two questions: How can it be measured, and does it matter? The distribution of character index scores (Fig. 6) showed that females never become as "hoary" as males. In fact, under the system I used to define male *exilipes* there would be no female *exilipes*. An *exilipes* male would have to be paired with a darker female. I have observed such mixed pairs of redpolls, but be-

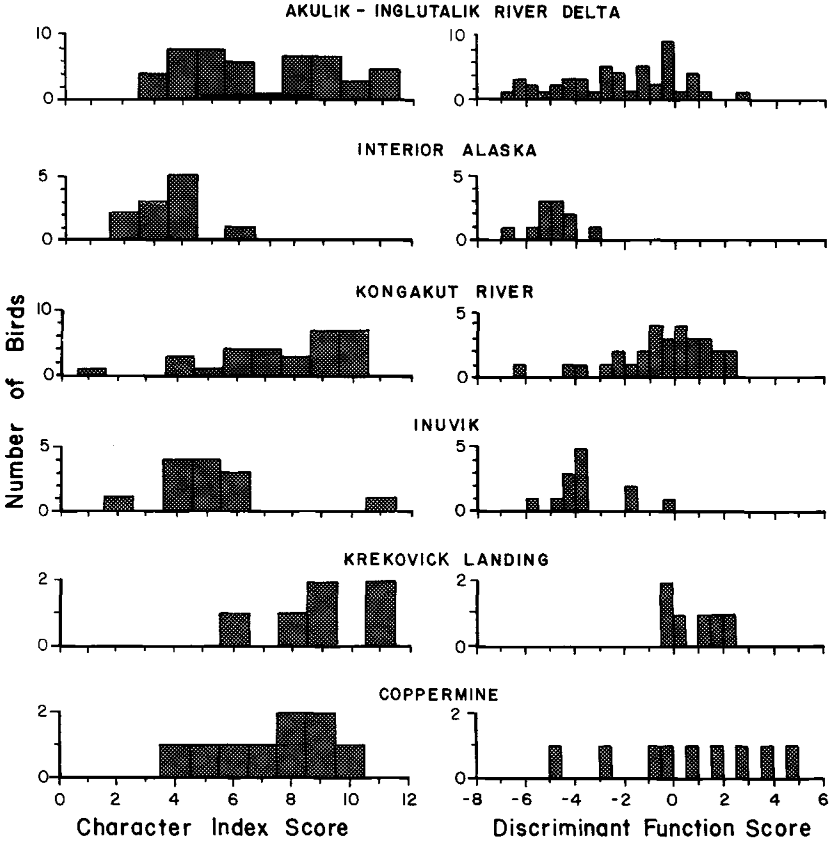

Fig. 8. Frequency distributions of character index and discriminant function scores of female redpolls.

cause of the absence of light-colored females, I have refrained from citing this as evidence of interbreeding. Any report of assortative mating is open to question unless a description of population variability at a location is presented and an objective means of defining the two taxa is used.

Even if assortative mating occurs, should it be used as evidence of species distinctiveness? I think not. Cooch and Beardmore (1959) demonstrated that positive assortative mating (association of similar plumaged individuals) occurred in a mixed population of the blue and white color morphs of Snow Geese (*Chen caerulescens*). Indeed, Cooke and Cooch (1968) hypothesized that assortative mating might be responsible for maintaining the polymorphism. Cooke (1978) found that Snow Geese selected mates similar in color to that of the family in which they were raised. O'Donald (1959) reported positive assortative mating among color morphs in Parasitic Jaegers (*Stercorarius parasiticus*). Klint (1978) found that coloration of the mother and siblings affected mate selection (again positive assortative mating) in normal and in white mutant Mallards (*Anas platyrhynchos*). Negative assortative mating has been demonstrated for the White-throated Sparrow (*Zonotrichia albicollis*; Lowther 1961, Thorneycroft 1976). Thus, I would suggest that, without supportive evidence, the argument of assortative mating is not necessarily useful in a discussion of the taxonomy of any pair of taxa since it is also an intraspecies phenomenon.

There is also a potential controversy over the type of redpoll occurring at some of the locations included in this study. In particular, there are published accounts that disagree with my finding of predominantly *flammea*-like birds at Churchill and Fort Chimo. Gabrielson and Wright (1951) found both taxa at Fort Chimo and listed *exilipes* as the more abundant form.

Similarly, Jehl and Smith (1970) listed both forms at Churchill; however, Jehl and Smith cited several studies that showed among-year variation in the proportion of *exilipes* at Churchill from 0 to 50%. My findings (unpubl.) of changes in abundance of the two forms between years are consistent with those of Jehl and Smith. That both extremes may occur sympatrically and interbreed in some years may account for the skewed distributions of predominantly *flammea*-type redpolls in some of my samples.

I conclude that *exilipes* and *flammea* represent the extremes of a single, highly variable species. This conclusion leads to questions regarding the reason for so much variability and for comparative adaptations of the extremes. These questions cannot be adequately answered at this time; some introductory information is available, however.

Wynne-Edwards (1952) could find no differences in habitat selection where the two forms were sympatric. Similarly, my samples from the Akulik-Inglutalik River delta and the Kongakut River were collected in relatively homogeneous habitats, yet both extremes were present. However, Jehl and Smith (1970) noted that at Churchill *flammea* was most common at tree line and *exilipes* in open areas (tundra). The large shift in frequencies of phenotypes from Inuvik (spruce forest) to Krekovick Landing (tundra) is in agreement with Jehl and Smith's observation. In general, *flammea* occurs throughout the range of *exilipes*; however, the converse is not true. At tree line and in more southerly areas, *exilipes* is rare or absent (e.g. in Interior Alaska, at Inuvik, and at Winisk).

The absence of *exilipes* from forested areas may indicate that it is poorly adapted in these regions, at least during the summer. Perhaps foraging adaptations are involved since one of the major morphological differences between *exilipes* and *flammea* is of bill size. Newton (1967) found a close association between bill dimensions (length and shape) and diet of *Carduelis* finches.

Other differences may be related to winter survival. Brooks (1968) found that *exilipes* possessed several minor physiological differences, when compared with *flammea*, that made it more tolerant of low temperatures. He suspected that there was a gradient in adaptation between the two extremes, i.e. that his findings did not indicate species differences. These physiological differences permit *exilipes* to winter farther north than *flammea* and, although not accounting for the plumage and morphological differences between *exilipes* and *flammea*, provide a mechanism for partially segregating the phenotypes during the winter. If this segregation extends into the early breeding season (for example until mate selection), this could contribute to the persistence of *exilipes*-type birds even in the absence of behavioral isolating mechanisms.

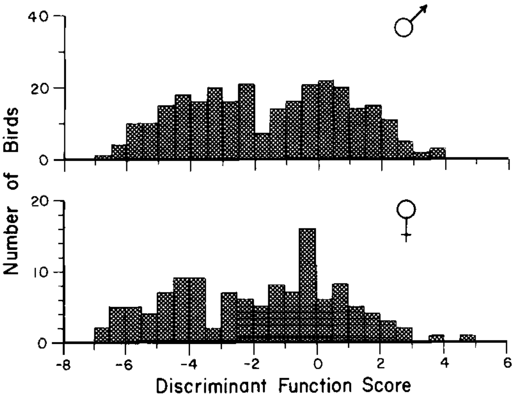

Fig. 9. Frequency distributions of scores along the discriminant axis maximizing the differences between *Carduelis f. flammea* (low scores) and *C. hornemanni exilipes* (high scores). All locations and plumage variants were pooled.

None of the factors discussed here provides an adequate explanation for the plumage differences found among redpolls, particularly when we take into account the present geographic distribution of the phenotypes. This problem is not unique to redpolls, as several other arctic and subarctic vertebrates, including Northern Fulmars (*Fulmarus glacialis*), Snow Geese, Rough-legged Hawks (*Buteo lagopus*), Gyrfalcons (*Falco rusticolus*), Pomarine Jaegers (*Stercorarius pomarinus*), Parasitic Jaegers, harbor seals (*Phoca vitulina*), and arctic foxes (*Alopex lagopus*) also have light and dark morphs that occur sympatrically yet vary in their relative proportions over the species' ranges. In none of these examples is a morphological difference known to be correlated with color phases.

This study has shown that all plumage types of redpolls are present at some breeding locations. This fact implies that the selection pressures that produced the present plumage characteristics are perhaps not operative in the

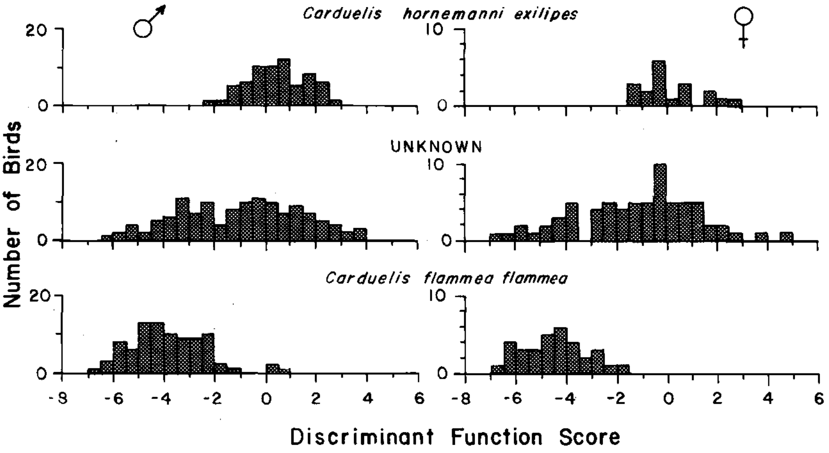

Fig. 10. Frequency distributions of scores along the discriminant axis maximizing the differences between *Carduelis f. flammea* and *C. hornemanni exilipes* for *flammea* and *exilipes* reference samples and for birds with intermediate plumage characters (unknown). All sample locations were pooled.

summer or may no longer exist. Salomonsen (1928) postulated that *flammea* and *exilipes* originated during the Pleistocene glaciation in separate areas in Asia—*flammea* in the interior region of southern Russia and *exilipes* in a refugium in central Siberia (*cabaret* probably was isolated in western Europe). If Salomonsen's hypothesis is true, the isolated redpoll populations may have acquired their differences during that period. As the climate moderated and the redpoll isolates expanded their ranges (including the colonization of North America) and became sympatric, their differences were insufficient to make them specifically distinct and interbreeding occurred, resulting in the continuum of characteristics we see now.

CONCLUSIONS

I have found no evidence to support the specific distinction of *flammea* and *exilipes.* These two taxa represent the ends of a continuum of plumage and skeletal variability. If they were once distinct species, hybridization has resulted in introgression to the extent that any species delimitation now is arbitrary. These findings are in agreement with those of Salomonsen (1928), Williamson (1961), and others who have studied redpolls in Greenland and Eurasia. I differ from some of these authors in that I would not recognize *exilipes* at the subspecific level. Subspecific recognition of *flammea* and *exilipes* would result in the awkward situation of sympatric subspecies, a condition generally not accepted by zoological taxonomists.

I recommend that *C. f. flammea* and *C. hornemanni exilipes* be merged into a single taxon for which the former is the correct name. Since similar conclusions regarding species distinctiveness have been reached in the study of other redpoll taxa [e.g. Salomonsen (1950) with *rostratus* and nominate *hornemanni*], it is appropriate to extend this merger beyond the limits of *flammea* and *exilipes* and to consider all redpolls one species, *Carduelis flammea.* Clarification of the taxonomic relationships of the subspecies *flammea, hornemanni, rostratus, cabaret,* and other named forms awaits further study.

ACKNOWLEDGMENTS

Many people aided in this study; I am grateful for their help. I was assisted in the collection of redpolls by Richard Gustafson, Leonard J. Peyton, Gerald F. Shields, Beverly DeVore, Elizabeth W. and Robert M. Burgess, and Alexander Elder. Jon C. Barlow and Jim Dick of the Royal Ontario Museum, Toronto, generously made materials in their collection available to me. I am especially grateful to those biologists who recognized the problems in redpoll taxonomy and had the foresight to collect series at various places across the Canadian Arctic. James D. Rising and his colleagues Frederick W. Scheuler and David M. Niles were responsible for most of these collections. Miriam L. Diamond collected the Krekovick Landing sample, as well as many of the Inuvik specimens.

Peter J. Bente kindly took the time to acquire a small sample from Kaktovik, Alaska.

Skeletonization of specimens collected in Alaska was made possible by the advice and facilities provided by Francis H. Fay of the Institute of Marine Science. Heinrich K. Springer generously provided me with a copy of plumage character states used in his unpublished research; this information provided the basis for the selection of variables and character states used in my study. I received help and advice in analysis from Edward C. Murphy, Frederick C. Dean, Curvin B. Metzler, and Robert M. Burgess.

Drafts of the manuscript (or the thesis from which it was extracted) were improved by the comments of Daniel D. Gibson, Dale R. Herter, Brina Kessel, Stephen F. MacLean, Edward C. Murphy, James D. Rising, Gerald F. Shields, and George C. West. I also appreciate the comments of the *Auk* reviewers: Richard F. Johnston, Kenneth C. Parkes, Dennis M. Power, and D. Scott Wood.

Field work at the Akulik-Inglutalik River delta was supported by a contract from NOAA (through the Outer Continental Shelf Environmental Assessment Program) to Gerald F. Shields and Leonard J. Peyton. The Chapman Fund generously supported field work in the Talkeetna Mountains and contributed to the museum work in Ontario.

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HUMMINGBIRD FLIGHT SPEEDS

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ABSTRACT.—Long-tailed Hermits (*Phaethornis superciliosus*) normally fly faster than the velocity predicted to minimize their cost of transport. The average speed we measured for individuals flying a known 40-m course was 11.5 m/s. Rapid flower visitation yields rewards that could compensate for the extra costs of fast flight. *Received 2 March 1984, accepted 30 July 1984.*

HOW fast should a bird fly? Intermediate flight speeds that minimize instantaneous power costs (V_{mp}), or more realistically that minimize the cost of flying a certain distance (V_{mr}), can be predicted from aerodynamic theory that is devoid of ecological context. The potential for minimization of power costs at intermediate speeds emerges from the U-shaped form of the relationship between power costs and flight speed (Fig. 1; Pennycuick 1969, 1975; Greenewalt 1975).

When can birds justify the extra energetic investment required for flight at speeds slower or faster than V_{mr}? The advantages of power dives, top-speed chases, and escape flights clearly outweigh the energetic sacrifices of brief high-speed flights. Stationary flight, such as hovering at flowers, also may yield net rewards (Pyke 1981). However, the natural flight speeds of birds in routine contexts rarely are compared to aerodynamic models. In one exceptional study Schnell and Hellack (1979) found that gulls and terns (Laridae) cruise near their colonies at velocities between V_{mp} and V_{mr}, i.e. at intermediate speeds at the bottom of the power curve.

The need for more such information is heightened by the recognition that time gained by flying fast may be used profitably in ways that compensate for the extra energy expended (Norberg 1981). Hummingbirds should be of particular interest in this context because of their sensitivity to the energetic consequences of alternative behaviors (DeBenedictis et al. 1978).

Previous analyses of the ecological correlates of hummingbird wing lengths have stressed the costs of hovering flight, a hummingbird specialty. The cost of hovering is a direct function of body weight and wing span (Greenewalt 1960a, 1975; Pennycuick 1969, 1975). Slight variations in wing lengths relative to body mass relate to differences in flight ecology (Feinsinger and Chaplin 1975, Feinsinger et al. 1979). Theoretically, forward flight speeds also should influence a hummingbird's flight costs and optimal wing lengths (Pennycuick 1969, Greenewalt 1975); however, these speeds have not been determined in an ecological context.

Here I consider the flight speeds of a 6-g hermit hummingbird, the Long-tailed Hermit (*Phaethornis superciliosus*). Hermit hummingbirds relate directly to the questions posed above because forward flight is the dominant component of their routine flight ecology. They fly considerable distances between dispersed flowers (Stiles 1979). Some species of hermit hummingbirds, including the species featured here, also commute frequently from lek display grounds to distant flowers. The estimates of flight speeds I present are the first for a hermit hummingbird and among the few natural flight speeds recorded for any hummingbird.

METHODS

This study was carried out in the lowland rain forest on the Osa Peninsula of Costa Rica. In June 1982 a single observer with a stopwatch timed flights of Long-tailed Hermits as they flew 40 m directly from one artificial flower to another along a broad trail. These hummingbirds visited the flowers regularly as a part of normal, daily trapline foraging. The observer sat near one flower, started the stopwatch when the hermit left it, and stopped the stopwatch as the bird pulled up to the distant flower. Arrivals were studied at the distant flower through 10× binoculars. Some slight error in judgment, reaction time, and parallax was inherent in these measurements. Minor acceleration and deceleration of unknown duration near the beginning and end of a flight make these measurements slight underestimates of true flight speed. We excluded times of flights during which the hummingbird veered off the trail and out of sight.

The wing lengths and masses of Long-tailed Hermits netted and marked on the Osa Peninsula in 1979–

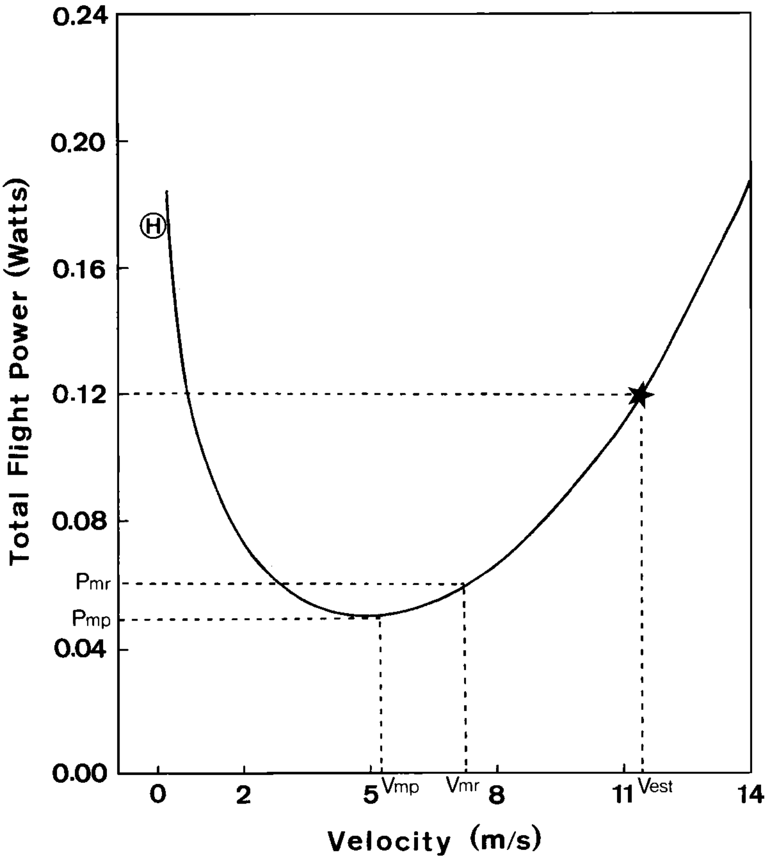

Fig. 1. Theoretical flight power curve for the Long-tailed Hermit calculated from Eq. 44 in Greenewalt (1975: 39). Minimum power velocity (V_{mp}) and maximum range velocity (V_{mr}) and associated power requirements for this species are indicated by dashed lines. *H* is the cost of hovering projected from Eq. 38 in Greenewalt (1975: 38). The position of the average flight speed (V_{est}) presented in this paper for the Long-tailed Hermit is indicated by a star.

1982 were 61.8 ± 0.2 mm and 6.3 ± 0.4 g ($n = 271$). These values fall close to the fitted regression for hummingbirds as a group (Fig. 2).

RESULTS

V_{mp} is about 5.5 m/s (20 kph) for all hummingbirds; the range of hummingbird body masses and wing spans is not sufficient to affect this greatly (Greenewalt 1975: 39). V_{mr} is higher [7.5 m/s (27 kph)] for hummingbirds. Using Greenewalt's Eq. 45 (1975: 39) for the Long-tailed Hermits studied, we projected V_{mp} to be 5.4 m/s and V_{mr} to be 7.3 m/s. The power requirements of this species flying at 1.4 m/s and 12.5 m/s should be about 3 times those at V_{mp} and only slightly less than the cost of hovering (Fig. 1).

The flight times we recorded averaged 3.47 s ($n = 10$, SD = 0.216, range 3.2–3.8 s), which calculates to an estimated average velocity of 11.57 ± 0.71 m/s (41.8 ± 2.56 kph). The Long-tailed Hermits flew 40 m in 5.3 s. These hermit hummingbirds flew not at V_{mp} or V_{mr}, but faster—at speeds of 2.1 × V_{mp} and 1.6 × V_{mr}, costing 72% of the energetic requirements of hovering at flowers (see Fig. 1). Our slowest recorded flight speed (3.8 s = 10.5 m/s) was 3.2 m/s faster than V_{mr} for this species.

Long-tailed Hermits also fly fast when they commute through relatively clear midstrata of the rain forest between lek territories and feeding areas up to 500 m away. The two flight speeds of commuting hummingbirds that we were able to measure were 10 and 11 m/s.

Field measurements of flight speeds with a

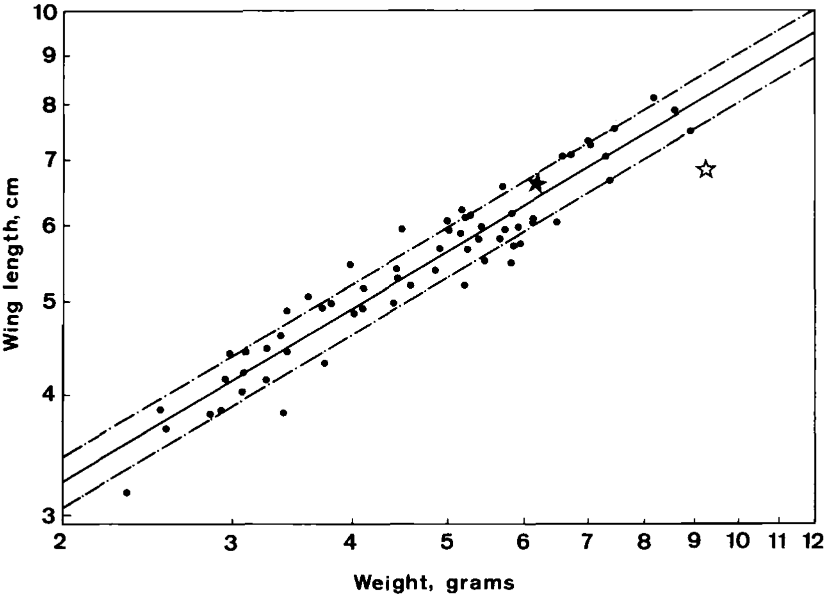

Fig. 2. Dimensions of hummingbirds for which sample sizes of more than 15 specimens were available (from Greenewalt unpubl.). Broken lines indicate 1 SD of the least squares regression, the equation for which is $\log L = 0.5973 \log M + 3.315$, and the standard deviation of the intercept = 0.0264. The average dimensions of the Long-tailed Hermit are indicated by a black star, while those of *Eutoxeres* are indicated by a white star.

stopwatch are estimates subject to several sources of error. Individual errors of reaction time or parallax, however, were at the level of 0.1–0.2 s or less, an order of magnitude less than the difference between estimated flight speed and V_{mr}. More detailed studies and larger sample sizes are needed to establish the flight speeds of Long-tailed Hermits precisely, but these data leave little doubt that they fly faster than V_{mr}.

DISCUSSION

It remains to be established that any hummingbird routinely flies at speeds that minimize its power costs. The few published records of hummingbird flight speeds vary greatly but do not suggest usual flight speeds at V_{mp} or V_{mr}.

Pearson (1961) released Allen's Hummingbirds (*Selasphorus sasin*) inside a highway drainage pipe and timed their escape speeds at 8 m/s (30 kph) and 11 m/s (40 kph). He concluded that normal cruising speeds of small hummingbirds were approximately 11 m/s (40 kph). Early reports of 21 m/s (75 kph) and 25–28 m/s (90–100 kph) (Hayes 1929, Allard 1934) by automobile-paced Ruby-throated Hummingbirds (*Archilochus colubris*) are not consistent with subsequent observations. Ruby-throated Hummingbirds, for example, could not progress against a 12 m/s (45 kph) headwind in wind tunnel experiments, suggesting that their maximum air speed was in this range (Greenewalt 1960b).

Wolf et al. (1976) reported that Green Violet-ears (*Colibri thalassinus*) flew 0.2–1.2 m/s (0.7–4.3 kph) between flowers less than 1 m apart. The linear relation of flight speed to distance in these data suggests that acceleration and deceleration constrained flight speed over such short distances. Montgomerie (1979) recorded speeds of 0.3–1.2 m/s by Cinnamon Hummingbirds (*Amazilia rutila*) flying short distances (less than 1 m) between flowers. Thus, slow flight speeds may characterize hummingbirds flying between adjacent flowers on a bush or hedgerow.

Norberg's (1981) ecological model of optimal flight speeds suggests that birds should increase their speed above V_{mr} when foraging, if the travel time saved compensates for the increased travel costs. The foraging ecology of Long-tailed Hermits provides this opportunity.

The 1.9 s saved by flying 40 m at 11.6 m/s instead of 7.5 m/s is close to the time a Long-tailed Hermit takes to extract nectar from one flower (Gill pers. obs.). The extra cost of flying 40 m between flowers at 11.6 m/s is roughly 0.144 J, whereas 1 μl of nectar in flowers the hermits typically visit (e.g. *Costus* and *Heliconia*) contains roughly 5 J. Extended to hundreds of flowers visited daily, the accumulated gain could be substantial.

There are two other features of the natural history of Long-tailed Hermits that potentially may be more important than simple energetic compensation. First, nectar rewards in the undefended, dispersed flowers these birds visit depend on which bird gets to a flower first. Individuals rarely have exclusive use of a particular flower (Gill pers. obs.). Even slight revisitation delay can result in loss of nectar to a competing individual. Second, male Long-tailed Hermits potentially sacrifice reproductive performance when they leave their lek territory (Stiles and Wolf 1979). Minimization of foraging time by means of fast flight and rapid flower visits should be advantageous if the time saved is used instead for lek activities.

Our evidence of fast flight in hermit hummingbirds also bears on the issue of adaptive wing-length variations in hummingbirds. Traplining hummingbirds that visit dispersed or low-yield flowers have longer wings and lower hovering costs than do territorial hummingbirds (Feinsinger and Chaplin 1975, Feinsinger et al. 1979). Paradoxically, some specialized trapliners, such as the hermit hummingbirds (Phaethorninae), do not have long wings and may even have shorter-than-average wings (Feinsinger et al. 1979).

There is no aerodynamic reason to expect high-speed trapliners, such as the Long-tailed Hermit, to evolve longer-than-average wings. Selection should favor longer-than-average wings in hummingbirds that fly slowly or that hover at low-yield flowers for much of their foraging time (Feinsinger et al. 1979). However, selection could favor shorter-than-average wings in hummingbirds that fly fast because shorter wings reduce power costs of profile drag, which increase with the cube of velocity (Pennycuick 1969, Rayner 1979).

Hermit hummingbirds as a group do not have shorter-than-average wing lengths. The relation between wing length (L, mm) and body mass (M, g) in a large sample ($n = 244$) of 130 hummingbird species spanning the family's size range (Greenewalt MS) is

$$\log L = 0.5186 \log M + 0.3891. \qquad (1)$$

The relatively longer wings of large hummingbirds compensate for their weight in such a way that their specific per-gram hovering costs are the same as those of small hummingbirds (Hainsworth and Wolf 1972, Greenewalt 1975). Hermit hummingbirds do not have atypical wing lengths, despite their various body sizes. The regression for hermits of the genera *Phaethornis, Glaucis, Threnetes,* and *Eutoxeres* is

$$\log L = 0.4724 \log M + 0.3966. \qquad (2)$$

The lower slope of this equation does not differ significantly ($d = 1.6110$, $P > 0.10$) from that of the equation for all hummingbirds excluding these hermit genera, namely,

$$\log L = 0.5647 \log M + 0.3735. \qquad (3)$$

Hermits of the genus *Eutoxeres* are aberrant, big (9–12 g) hummingbirds with short wings that correspond in length to those of hummingbirds about 7 g in mass. Instead of hovering, they usually cling to *Heliconia* bracts while feeding. Their wing lengths certainly do not relate to efficient hovering. The regression of wing length vs. mass for hermits excluding *Eutoxeres* is even more similar to Eq. 3:

$$\log L = 0.5092 \log M + 0.3760. \qquad (4)$$

The high average wing disc loading of hermit hummingbirds mentioned by Feinsinger et al. (1979) apparently was the result of including *Eutoxeres* in their sample of "hermits"; the average value of their data set excluding *Eutoxeres* (by my calculations) was not significantly different from other groups of hummingbirds.

Variations in wing disc loading and hovering power requirements discussed by Feinsinger and Chaplin (1975), Feinsinger et al. (1979), and others are departures from the average trend, the variance about the regression rather than the slope of the regression itself. However, this variance (Eq. 1) is not great; the standard deviation of the intercept is 0.0393. Conceivably, some traplining hermit hummingbirds have higher wing disc loadings than other species with which they coexist, a result perhaps of local sorting of species with different foraging strategies and corresponding wing lengths (Feinsinger et al. 1979). If this proves to be the case, details on flight speeds would be needed to determine whether flight power considerations were involved in any way. The short wings of territorial hummingbirds (see Feinsinger and Chaplin 1975), for example, probably relate to the ability to accelerate and maneuver in chases and displays rather than to energetic considerations.

ACKNOWLEDGMENTS

I am especially grateful to C. H. Greenewalt, who prodded my thinking away from energetics and who made available unpublished analyses of hummingbird dimensions. R. Montgomerie, F. G. Stiles, and C. L. Gass generously provided access to unpublished manuscripts. P. Feinsinger, C. L. Gass, F. R. Hainsworth, J. P. Myers, and L. L. Wolf criticized early drafts of this paper. R. Ray, A. Mack, D. Wechsler, F. Joyce, P. Marcotullio, and D. Emery assisted in the field. I am indebted also to the staff of the Servicio de Parques Nacionales of Costa Rica for their many courtesies and their assistance in Parque Corcovado. I extend special thanks to A. Ugalde, F. Cortez, J. Gamboa, H. Delgado, and M. Felis.

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Nominations for Elective Members and Fellows of the A.O.U. may be made up until 5 months prior to the next stated meeting. Nominations of Fellows must be signed by three Fellows. Nominations of Elective Members must be signed by three Fellows or Elective Members. The number of Fellows under 60 years of age is restricted to 75 by the bylaws. However, the number of new Elective Members each year is in large part determined by the number nominated—we can elect up to 75% of the nominees. Prescribed forms may be obtained from the Secretary (see inside front cover of *The Auk* for address). Completed forms must be returned to the Secretary by **7 May 1985** in order to be eligible.

Nominations for officers may be made in writing to the Secretary at any time prior to the next meeting of Fellows and Elective Members, which is 7 October 1985. The following positions will be vacant in 1985: Vice President and three Elective Councilors.

AN ANALYSIS OF PLUMAGE AND MORPHOLOGICAL CHARACTERS OF THE TWO COLOR FORMS OF THE WESTERN GREBE (*AECHMOPHORUS*)

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ABSTRACT.—The dark and light color forms of the Western Grebe (*Aechmophorus occidentalis*) are defined in this study by bill color. Considerable overlap between the phases was found in all plumage color characteristics except facial patterns. The feathers of the head are molted twice annually, and most facial intermediacy of juvenile and wintering birds disappears as the breeding season approaches. Most body feathers are molted once, except those of the flanks, scapular region, and base of the leg, which appear to be in a state of molt throughout the year. These feathers, especially those of the flanks, are believed to be those ingested regularly by the birds. Some birds molt the remiges with the annual (Prebasic) molt in late summer, but some, possibly birds in their first winter, molt them in midwinter. The measurement data indicate that the dark-phase birds on Clear Lake, California are larger and may be descendents of wintering birds from the north. *Received 3 April 1984, accepted 24 August 1984.*

THE two color forms or phases of the Western Grebe have been known since Lawrence (*in* Baird 1858) originally described them as two species, the dark-faced form as *Podiceps occidentalis* and the light-faced form as *P. clarkii* (Fig. 1). Until recently, they generally have been considered color phases of a single species, *occidentalis,* for which the genus *Aechmophorus* was erected by Coues (1862). Dickerman (1963) separated the small Mexican birds as a distinct subspecies, to which he applied the name *Aechmophorus occidentalis clarkii,* selecting one of Lawrence's cotypes as lectotype.

Storer (1965) reported assortative mating in these grebes, the birds usually selecting mates of their own color phase. Subsequently, Feerer (1977) presented comparative data on prey size and color patterns, plus an analysis of measurement data from a large series of Western Grebes from Clear Lake, Lake County, and Topaz Lake, Mono County, California collected in the late 1960's by Herman and Rudd for pesticide residues (Herman et al. 1969). Ratti (1979) presented further information on assortative mating, evidence for ecological segregation, color differences in the young, and possible isolating mechanisms. Nuechterlein (1981) demonstrated that the assortative mating resulted from differential responses to the phase-specific Advertising calls, which are single-noted in the light-phase birds and double-noted in the dark-phase birds.

Most of the birds Feerer (1977) reported on were kept frozen until August 1981, when Herman kindly gave them and other frozen California specimens to The University of Michigan Museum of Zoology (UMMZ). There they were prepared as specimens, and they form the primary basis for this report.

In the United States and Canada, Western Grebes show a clinal decrease in wing length from north to south. There is also an increase in the relative frequency of the light-phase birds in the south, from less than 1% of the population in Canada (Storer 1965) to 12–18% in Utah (Storer 1965, Ratti 1979) to more than 50% in Mexico (Dickerman 1973). Yet even within a local area, major differences exist in the proportion of light- and dark-phase birds from one lake to the next (Feerer 1977, Ratti 1979, Nuechterlein unpubl. data). It is evident that a large sample from a single, mixed population is needed for accurate analysis of the differences between the two forms. The Herman-Rudd sample of 111 birds from Clear Lake (39°N) and 47 from Topaz Lake (38°43′N) has provided such an opportunity.

In addition to describing geographic and intermorph differences in this complex, we have asked several questions: How much interme-

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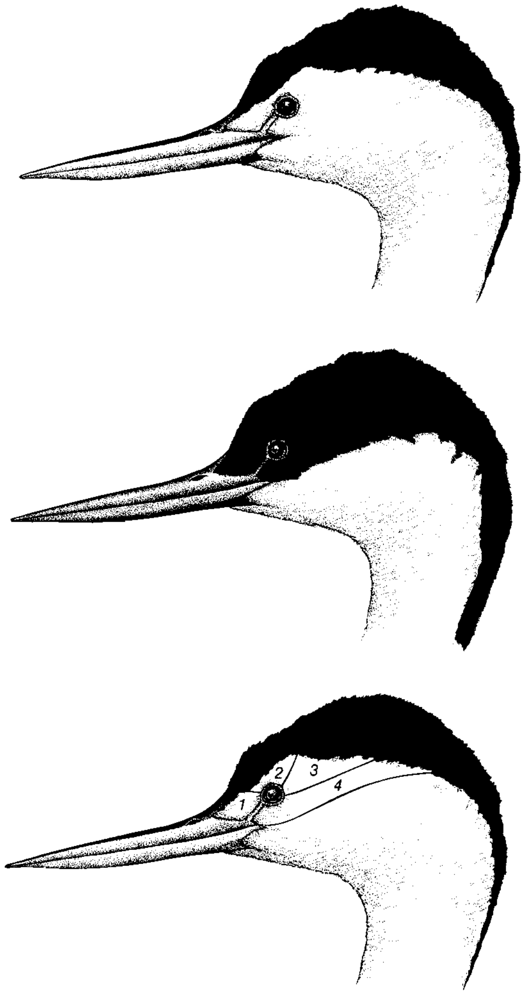


Fig. 1. Heads of light-phase (top) and dark-phase (middle) male Western Grebes. Bottom drawing shows areas into which the face was divided for analysis of pattern in the Clear Lake series (1 = lores, 2 = above eye, 3 = behind eye, 4 = below eye).

diacy is there between the forms, and how can this intermediacy be explained? Which color characters are consistent within each phase? What morphological characters might be associated with ecological differences in locomotion and foraging behavior between birds of the two phases?

Materials and Methods

The birds received from Herman were kept frozen until prepared. After thawing, each bird was measured by Storer as follows: wing length (arc) was measured on a mm rule, and tarsal length, bill length from the anterior edge of the nostril to the tip, and bill depth at the level of the posterior edge of the nostril were taken to the nearest 0.1 mm with dial calipers. The heads were then photographed in black and white. The birds were cut down the midventral line, skinned, the fat removed by scraping and soaking in Stoddard's solvent, and the pelt pinned out flat to dry. One wing of each bird had been removed before we received the birds, so the bones from the other wing were removed and saved with the rest of the skeleton, as were the bones of one foot. The pelts were used for the study of molt, age, and seasonal differences in plumage, as well as differences in the amount of dark and light in the plumage.

Data used for the study of geographic variation were taken by Storer on visits to approximately 100 collections in the United States, Canada, and England, where 540 specimens were examined and measured. Most of the specimens also were classed as light or dark phase on the basis of bill pattern and compared with a series of 6 sketches of various head patterns (Fig. 2). The measurements were the same as those taken on the Herman series. However, because the Herman birds were not dried when measured, their measurements were not combined with those of the museum skins for this analysis. For statistical analyses, we used Chi-square and two-tailed *t*-tests.

Aging.—The bursa of Fabricius (Bursa cloacalis, Baumel 1979), which is maintained but reduced in size through the first breeding season (Nuechterlein unpubl. data), is the best method available for aging Western Grebes. Because bursa data were not taken on the Herman series, we examined skeletons of the Herman series for characters that varied with age. The tarsometatarsus is the last major skeletal element to become completely ossified in grebes. The region near the fusion of the proximal epiphysis and the shaft is rough (pitted or grooved) until the birds are several months old (Storer pers. obs.). Virtually all of the 119 skeletons of Western Grebes that Nero (1960) found frozen in Lake Newell, Alberta, and deposited at UMMZ can be aged by this criterion. Assuming that most of these birds were hatched in mid-June, they were approximately five months of age when they died in mid-November.

The Pons supratendineus also was used in aging. This is a bridge on the anterior surface of the distal part of the tibiotarsus that lies across the tendon of M. extensor digitorum longus. It is cartilaginous in young birds and completely ossified in adults.

Molt.—The preparation of the Herman series as flat pelts permitted us to detect growing feathers from the underside of the skin. Each pelt was divided into ten areas: crest, face, throat, neck, back, flanks, belly, humeral tract, interscapular tract, and base of leg. For each area the stage of the molt was recorded as none (0), light (1), moderate (2), or heavy (3). As in other

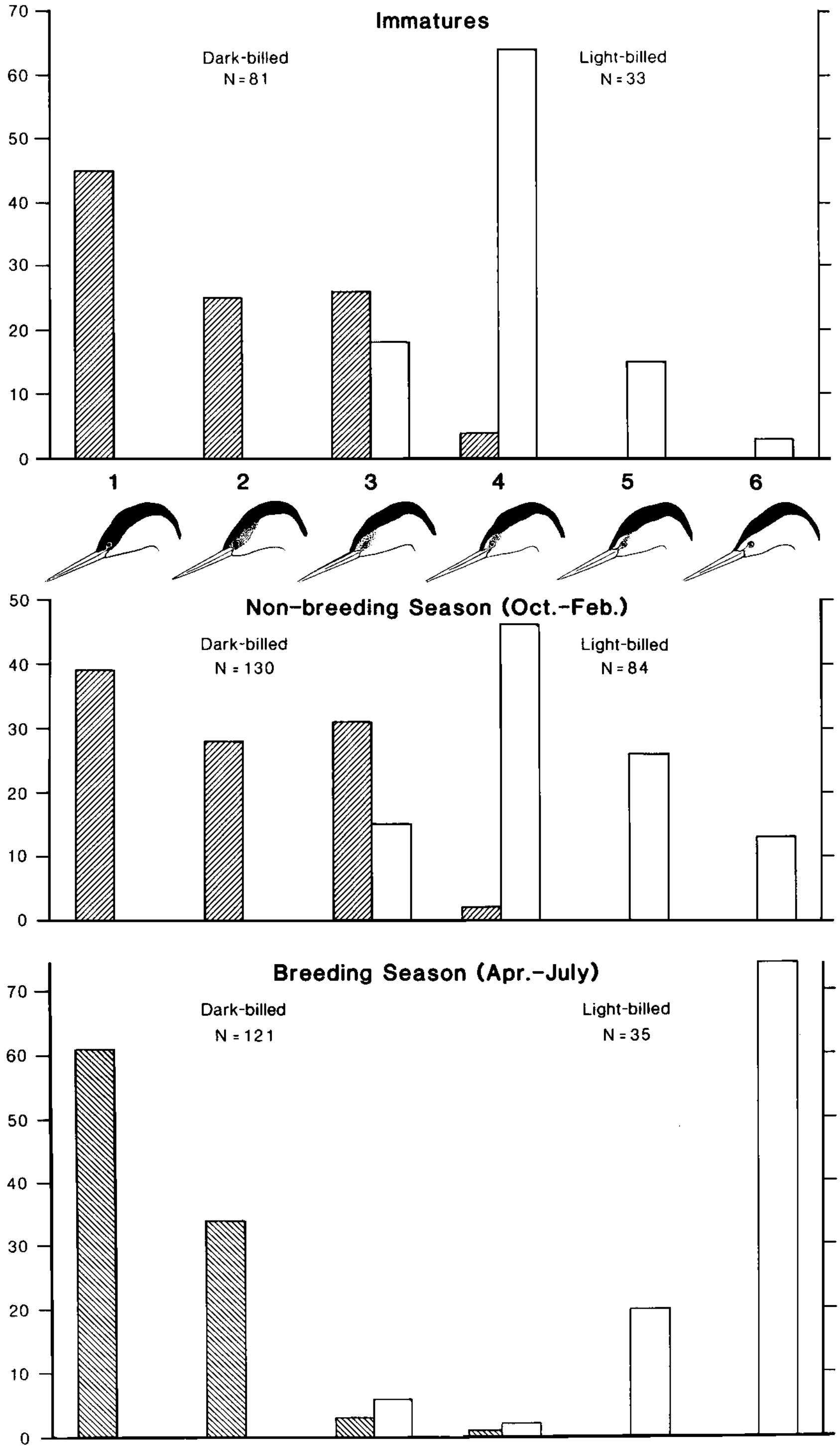


Fig. 2. Distribution of facial patterns by age, season, and color phase (data from museum skins).

TABLE 1. Geographical variation in Western Grebes.

	Mexico		Southern U.S.		Northern U.S.		Canada	
	n	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)
Males								
Wing length	18	186.7 (4.34)	18	196.9 (5.47)	39	201.5 (5.73)	32	205.8 (4.68)
Tarsal length	19	72.92 (3.01)	18	77.61 (2.97)	36	77.86 (2.75)	33	77.76 (2.48)
Bill from nostril	19	55.49 (2.76)	16	60.48 (2.82)	33	60.83 (2.83)	30	62.73 (3.33)
Bill depth	19	11.86 (0.50)	16	13.04 (0.65)	34	12.93 (0.71)	30	12.70 (0.62)
Females								
Wing length	14	174.1 (4.37)	13	184.4 (3.48)	21	190.5 (5.40)	26	192.4 (5.21)
Tarsal length	16	66.62 (1.91)	14	71.58 (1.70)	21	71.43 (2.51)	26	71.14 (3.31)
Bill from nostril	15	46.99 (2.58)	14	52.20 (2.20)	17	53.30 (2.65)	25	53.45 (2.69)
Bill depth	14	9.35 (0.48)	11	10.17 (0.69)	20	10.29 (0.74)	25	9.95 (0.73)

grebes, the remiges are molted simultaneously. The condition of these feathers was recorded as out (0), partially but less than half grown (1), more than half but not fully grown (2), or fully grown (3).

Skeletal measurements.—In addition to the measurements taken on the birds before preparation, the following measurements were made with dial calipers to the nearest 0.1 mm: the overall length of the ulna, femur, tibiotarsus, tarsometatarsus, and all but the ungual phalanges of the toes; the widths of the proximal and distal ends of the femur, tibiotarsus, and tarsometatarsus; the least width of the shaft of the last three elements; the length of the cnemial crest of the tibiotarsus; and the height and basal width of the patella. The lengths of the second, third, and fourth toes were estimated by adding the lengths of the phalanges (excluding the ungual ones). This gives a somewhat higher figure than the sum of these bones when articulated but is just as useful for the comparisons that we made.

Color characters.—For all plumage color characters analyzed except color over eye (which was either black or white), we selected a graded series of two to seven reference specimens. The specimens in each group were assigned consecutive numbers, beginning with 1 for the darkest state for the character. The characters, their states, and the UMMZ catalogue numbers of the reference specimens for each character are listed in the Appendix. The extent of plumage variation within and between the two color phases was determined by comparison of each pelt of the Herman series directly with those of each reference series, and we jointly assigned to it the number of the reference specimen it most closely matched. We did not analyze variation in the back feathers and their edgings (Storer 1965) because of seasonal changes due to wear and fading.

For the computer analyses we separated the specimens into the light and dark phases using bill color, which does not change with season. The bills of dark-phase birds have a layer of melanin that is diffused throughout the insides of both the upper and lower rhamphothecae. This gives the bill the dull yellowish-green appearance in life, rather than the bright orange-yellow of light-phase birds. The melanin of the bills of light-phase birds is largely confined to a narrow strip along the dorsal part of the upper rhamphotheca. From the outside, this dark strip contrasts sharply with the rest of the bill. Intermediates between these two types were rare and usually were immature birds. Long periods of freezing or drying may cause large irregular blotches of yellow to appear on the bills of dark-phase birds, presumably because the inside melanin layer separates from the rhamphotheca. For this determination, we therefore removed the rhamphothecae from the bills and viewed them from the inside.

RESULTS

GEOGRAPHIC VARIATION

Museum specimens taken in the breeding season were divided into four populations: Mexico exclusive of Baja California, Baja California and the United States south of 40°N, the United States north of 40°N, and Canada. (Further subdivisions were not made because of the paucity of breeding birds in the museum samples.) The sample sizes, means, and standard deviations for the four measurements for each population are shown in Table 1.

The Mexican birds were smaller than those of all the more northern populations in all measurements (two-tailed *t*-tests, $P < 0.001$). In the three northern populations there is a cline of increasing wing length from south to north. The differences between males in adjacent populations were significant at the 0.01 level, as were those between females of the southern and northern United States populations. Although the difference between the northern

TABLE 2. Size (mm) vs. color phase in the Mexican population.

	Dark phase		Light phase		Significance level (*t*-test)
	n	Mean (SD)	*n*	Mean (SD)	
Males					
Wing length	5	185.0 (2.45)	11	188.1 (4.46)	0.17
Tarsal length	6	72.08 (2.45)	11	73.54 (3.50)	0.38
Bill from nostril	5	55.56 (2.04)	12	55.02 (3.01)	0.72
Bill depth	5	11.98 (0.53)	12	11.73 (0.45)	0.33
Females					
Wing length	6	174.3 (4.18)	8	174.0 (4.78)	0.89
Tarsal length	6	67.22 (1.88)	10	66.26 (1.93)	0.35
Bill from nostril	6	47.20 (1.11)	9	46.86 (3.29)	0.81
Bill depth	6	9.55 (0.59)	8	9.20 (0.34)	0.19

United States population and that of Canada was in the same direction, it was not statistically significant.

Neither of the two northernmost samples contained enough light-phase birds to test for differences between the phases. Therefore, only the Mexican and Clear Lake samples were used. In the small Mexican sample, there were no significant differences between the phases (Table 2). In the Clear Lake sample, the dark birds averaged larger than the light birds in all four dimensions. Differences in tarsal length in both sexes and in bill depth in females were not significant (Table 3). In most measurements, the dark-phase birds were more like the birds from the northern United States or Canada, and light-phase birds like those from the southern United States. This suggested that many of the dark-phase birds collected on Clear Lake may have been wintering birds from northern populations. However, dark-phase birds taken in the breeding season (May–October) showed similar results.

AGING

The breeding season for Western Grebes on Clear Lake is much longer than in Canada. This was reflected in our finding birds in the Herman sample with incompletely ossified tarsometatarsi from 14 August to 27 March. In one bird taken 28 December at Clear Lake, the proximal epiphysis was not yet fused to the shaft of the bone. The length of the breeding season and consequently the occurrence in winter and spring of young birds differing as much as six months in age complicated the analysis of molt in the Clear Lake sample.

In 168 of 180 birds, the ossification of the Pons supratendineus was in agreement with the ossification of the tarsus. Of these, 146 were "adults" and 22 immatures. In 5 of the remaining 12, the tarsometatarsus showed the adult condition, and the bridges on one or both sides were incompletely ossified. This indicated that ossification of the supratendineal bridge may be completed later than that of the tarsometatarsus. The condition of the remaining seven birds was not clear, but of these, only one appeared not to follow the general pattern. It was a bird with a possibly unfused tarsometatarsus and a probably ossified bridge. Oddly, asymmetry was apparent in the amount of ossification of the bridge in five birds: either the bridge on the right or left tibiotarsus was noticeably more ossified than its mate.

MOLT

The molts and plumages of the Western Grebe have not been well described. What has been known was summarized by Palmer (1962: 95). The Definitive Alternate (adult nuptial) plumage is "acquired by [a] Prealternate molt in spring, involving (so far as is known) mainly [the] head and neck." The Definitive Basic (adult winter) plumage is "acquired by [a] complete Prebasic molt in fall, the flight feathers shed simultaneously (a flightless period). A bird flightless in midwinter, owing to molting of rectrices [sic], was examined by J. Munro (W. E. Godfrey) .... In spring, a partial molt [in first-year birds] produces the black crown .... 'In this first nuptial plumage adults and young are practically indistinguishable.'" Subsequently, Sibley (1970: 373) found Western

TABLE 3. Size (mm) vs. color phase in the Clear Lake population.

	Dark phase		Light phase		Significance level (*t*-test)
	n	Mean (SD)	*n*	Mean (SD)	
Males					
Wing length	34	203.4 (3.81)	15	198.6 (3.56)	0.001
Tarsal length	41	78.14 (2.49)	18	77.44 (2.41)	0.32
Bill from nostril	35	62.61 (2.58)	17	60.25 (2.48)	0.003
Bill depth	39	13.59 (0.60)	18	12.97 (0.49)	0.001
Females					
Wing length	22	190.0 (5.34)	13	183.9 (3.33)	0.001
Tarsal length	25	71.70 (1.96)	14	71.35 (1.36)	0.56
Bill from nostril	22	53.16 (2.59)	14	50.41 (2.21)	0.003
Bill depth	22	10.47 (0.42)	14	10.21 (0.43)	0.081

Grebes with molted or growing primaries in late January and early February in southern California.

Remiges.—Specimens of grebes taken in the period of molt and regrowth of the remiges are rare (Stresemann and Stresemann 1966), and the timing of the molt of the remiges in grebes is not well established. The California sample obtained from Herman is remarkable in containing 21 birds in various stages of the molt and regrowth of the remiges. Adult males with freshly molted remiges were taken 24 July (1), 31 August (2), 21 September (2), and 18 October (1) and with growing remiges 31 July (1), 14 (1) and 21 (2) August, and 5 (1), 21 (2), and 23 (1) September. Adult females with freshly molted remiges were taken 24 July (1) and 31 August (2) and with growing remiges 21 August (2) and 5 September (2). In addition, a female from Santa Barbara with partially grown remiges was taken 1 February 1969. It is thus evident that the remiges are molted by some birds in midwinter and by others in late summer. The age of birds molting in midwinter is unknown.

Thirteen birds with adult skeletal characteristics had worn primaries in the period from 21 June to 23 September, and one had fresh primaries by September. Two probable adults had worn primaries on 17 July and one, fresh primaries on 21 September. Six possible one-year-olds had fresh primaries in the period from 17 July to 15 September. Thus adults go into the breeding season with worn primaries, presumably grown the preceding summer, whereas at least some yearlings begin the breeding season with fresh primaries. These may be birds that have had a midwinter molt of the remiges. It is unclear whether these birds again molt their remiges in summer, six months or so after the midwinter molt. Two birds from the Herman sample (UMMZ numbers 204,564 and 204,567) taken 5 September and 21 August were growing their remiges, but the evidence for their being yearlings was not entirely convincing.

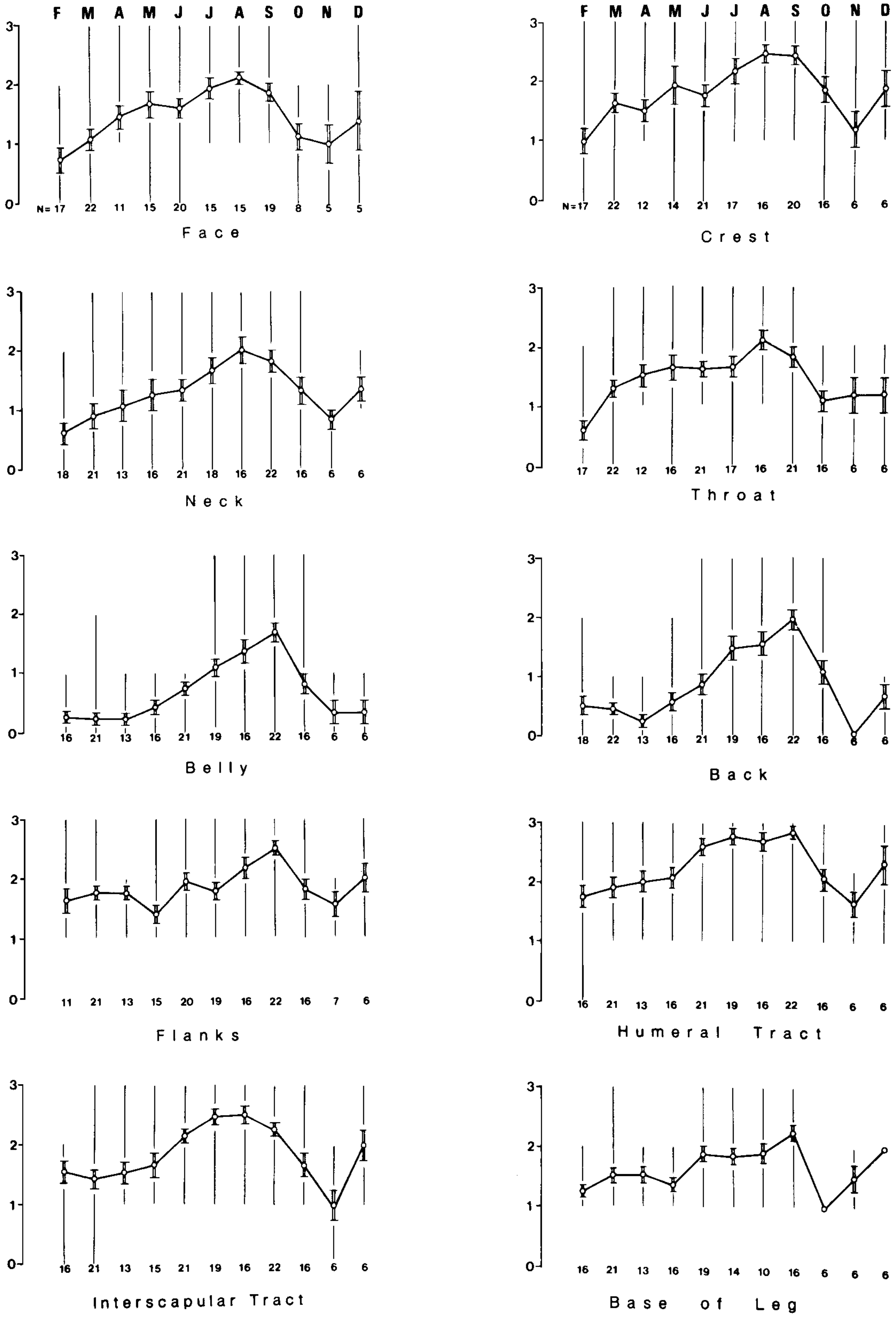
Crest.—Birds with the crest in the process of molt were found throughout the year, and only 6% of the sample showed no molt in this area. The peak of the molt occurred during the period of the annual molt, June through October, but there was also considerable molt of the crest from March through May, the latter presumably the prenuptial (Prealternate) molt suggested by Palmer (1962: 95). (For mean monthly scores for molt of this and other areas, see Fig. 3.)

Face.—The molt pattern of the face was similar to that of the crest, although the rankings were somewhat lower. This is also consistent with the occurrence of a prenuptial molt.

Throat.—The molt pattern of this area was hardly distinguishable from that of the face.

Neck.—Some birds were growing neck feathers each month, but the peak of the molt coincided with the annual molt, being greatest from July through September.

Belly.—The molt of the belly feathers was rarely more than light, except at the time of the annual molt (July through September). These feathers evidently are molted once a year and, compared with other tracts, in relatively small numbers at any time. These are the feathers that are constantly in contact with the water and presumably are of vital importance in keeping water from penetrating to the skin. For this reason, selection can be expected to have favored a molt of few feathers at a time rather



Face

Crest

Neck

Throat

Belly

Back

Flanks

Humeral Tract

Interscapular Tract

Base of Leg

than an extensive molt that might radically reduce waterproofing. In this connection, it should be noted that the belly feathers also are the first to develop in young grebes.

Back.—The seasonal molt pattern of the back was similar to that of the belly, but there were relatively more birds in the heavier molt categories. This shift may reflect less rigorous selection for a gradual molt like that in the molt of the belly feathers.

Flanks.—Some flank feathers were growing in all birds in the series, moderate molt being the most frequent category. In only one month (May) was light molt (1) more frequently found, and in one (September) heavy molt (3) was the most frequent. Virtually every grebe of all species that Storer has examined (unpubl. data) has had growing flank feathers. These feathers are presumably a major source of those swallowed by the birds and retained either in the lumen of the stomach or as the separate pyloric plug (Storer 1969: 185).

Humeral tract.—Like the flanks, this area (with one exception) was always in molt, and it was the only area in which heavy molt (3) was the most frequent category. Heavy molt was found in every month except November. [The small sample for that month (6) probably accounts for this discrepancy.] Also, like the flanks, this tract probably is a major source of feathers for the stomach.

Interscapular tract.—This tract also appeared to undergo molt almost constantly. Only 4 of 171 birds (2.3% of the sample) showed no molt in this area. Light molt predominated in most months, but the peak of the molt coincided with the annual molt, occurring from June through September.

Base of leg.—The area around the distal end of the tibiotarsus was constantly in molt. The light molt category (1) was the most frequent, except during the period of the annual molt (June through September).

COLOR CHARACTERS—HERMAN SERIES

Facial characters (Figs. 1, 4).—The border separating the black and white feathers on the face frequently intersected the eye on nonbreeding adults. Such intermediacy in facial plumage (character state 2) was especially common for light-phase birds, for which it was the most frequent character state (Fig. 4). However, adults taken in the breeding season (here defined as from late April–October) showed little intermediacy and no overlap.

In all 87 dark-phase birds, the black of the top of the head either intersected or came below the eye. Only 1 of 20 adult light-phase birds in the breeding season had this character state, but outside the breeding season 15 of 31 adults and 10 of 12 immatures of the light phase were similar to the dark-phase birds in this state.

Breeding birds showed no overlap in the color pattern behind the eye. All dark-phase birds were rated 1, 2, or 3, whereas all light-phase birds were rated 5. Outside the breeding season 2 of 35 dark adults, 1 of 10 dark immatures, 14 of 30 light adults, and 11 of 13 light immatures were ranked 4, indicating a moderate degree of overlap.

Breeding adults showed no overlap in the color below the eye. All dark birds were rated 1, 2, 3, or 4, whereas all light adults were rated 6. In the nonbreeding season there was a shift of light-phase birds toward the dark phase: 11 of 31 adults and 9 of 12 immatures were ranked 5. The only overlap was a light-phase immature that was rated 4, as were 11 dark-phase birds, 6 adults and 5 immatures.

Breeding adults showed a complete segregation by color phase in the color of the lores. Dark-phase birds all had dark or light gray lores, whereas light-phase birds all had white lores. This segregation also held for the nonbreeding season, with the single exception of a light-phase juvenile with light gray lores taken 28 November.

Mottling of the lores was uncommon. In the breeding season, only two (both dark phase) of the 62 adults had this character state. The sample from the rest of the year had a higher proportion of birds with mottled lores: 1 of 34 dark adults, 1 of 11 dark immatures, 2 of 30 light adults, and 5 of 13 light immatures. The differ-

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Fig. 3. Mean monthly molt scores for various parts of the body (phases combined). Bars show standard error and ranges. Ordinal scores ranged from 0 (no molt) to 3 (heavy molt). No birds were collected in January.

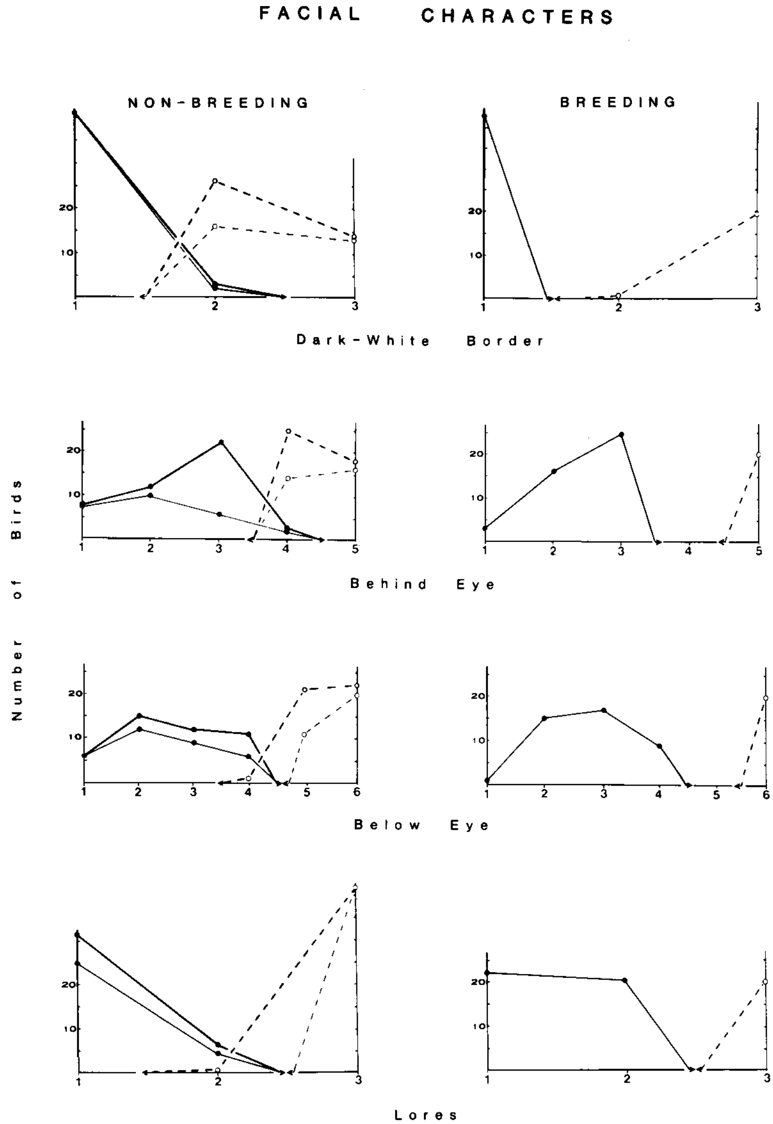

Fig. 4. Distribution of four facial color characters by color phase and season. Solid lines represent dark-phase (dark-billed) birds; dashed lines, light-phase birds. Heavier lines and dashes on graphs of nonbreeding birds represent total sample, lighter lines and dashes total adults. Arrows indicate that no birds were assigned to remaining color states. Numbers on abscissa represent states of color characters (darkest state of each is on the left; see Appendix for description of states).

ences between light adults and immatures were significant ($\chi^2 = 7.6$, $P < 0.05$), but mottling occurred in both age groups of both phases.

Other characters (Figs. 5, 6).—There was complete overlap between the phases in the amount of gray or white at the base of the crest, although the dark birds tended to have darker bases (85 of 90 birds in the two darkest classes). These trends apparently were not related to season or age, although light juveniles had a relatively higher proportion in the lightest category (4) and a lower proportion in category 3 than adults.

The amount of white at the base of the scapulars tended to sort out by phase, with considerable overlap. About 23% of the dark birds and

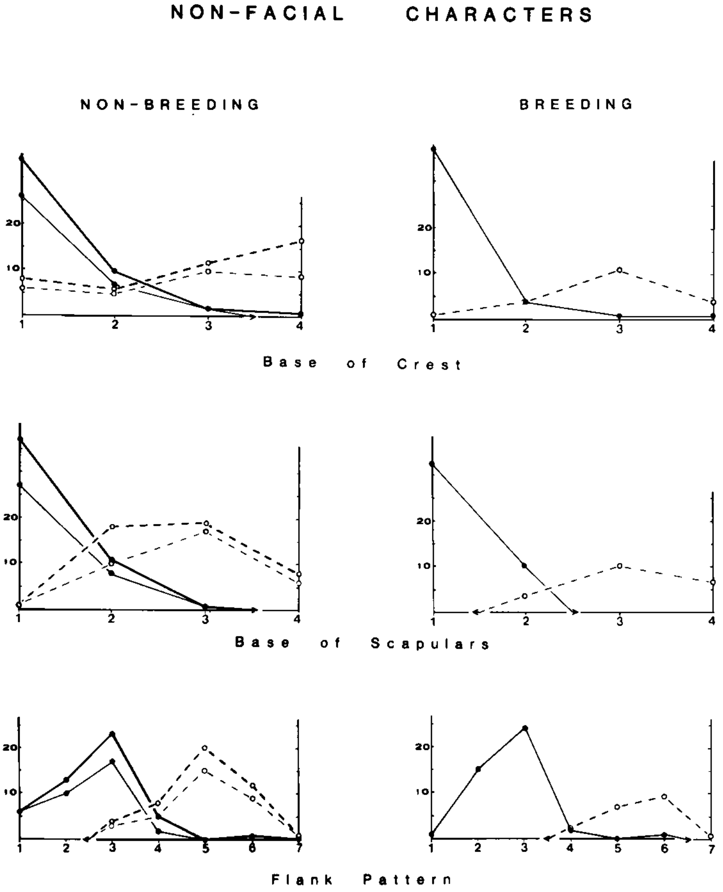

Fig. 5. Distribution of three nonfacial body characters by color phase and season. For explanation of symbols and lines, see legend to Fig. 4.

38% of the light birds were in category 2 (of 4). No conspicuous seasonal differences were apparent.

The flank pattern varied greatly, but few birds had either the dark or light extremes of the 7 categories. Again there was considerable overlap, but there were concentrations of dark birds in the dark categories (72 of 81 in categories 1-3) and of light in the light categories (50 of 65 in categories 5-7). There were no conspicuous age or seasonal differences. In addition to the variation from dark to light, there was much individual variation in the pattern of the dark spots. Such individual variation may be used by birds as individual identification marks.

The amount of white in the lesser upper wing coverts showed a large overlap between the phases (Fig. 6). Although 60% of the dark birds were in category 1 (of 4) and 50% of the light birds were in category 3, 36% of the birds in each phase were in category 2.

The lesser underwing coverts also showed complete overlap, some birds of each phase being in each category. The majority (53%) of the dark birds and 25% of the light birds were in the intermediate category, whereas the majority of the light birds (72%) was in the lightest category (3) with 12% of the dark birds.

The greater underwing coverts were unique among the characters studied in that the greatest number of birds in both phases was found in the lightest category (3). There was still a tendency, however, for more dark birds to be in the darker categories. There appeared to be no consistent age or seasonal differences in the distribution of any wing-covert character by color phase.

The wing pattern (Figs. 6 and 7) also varied

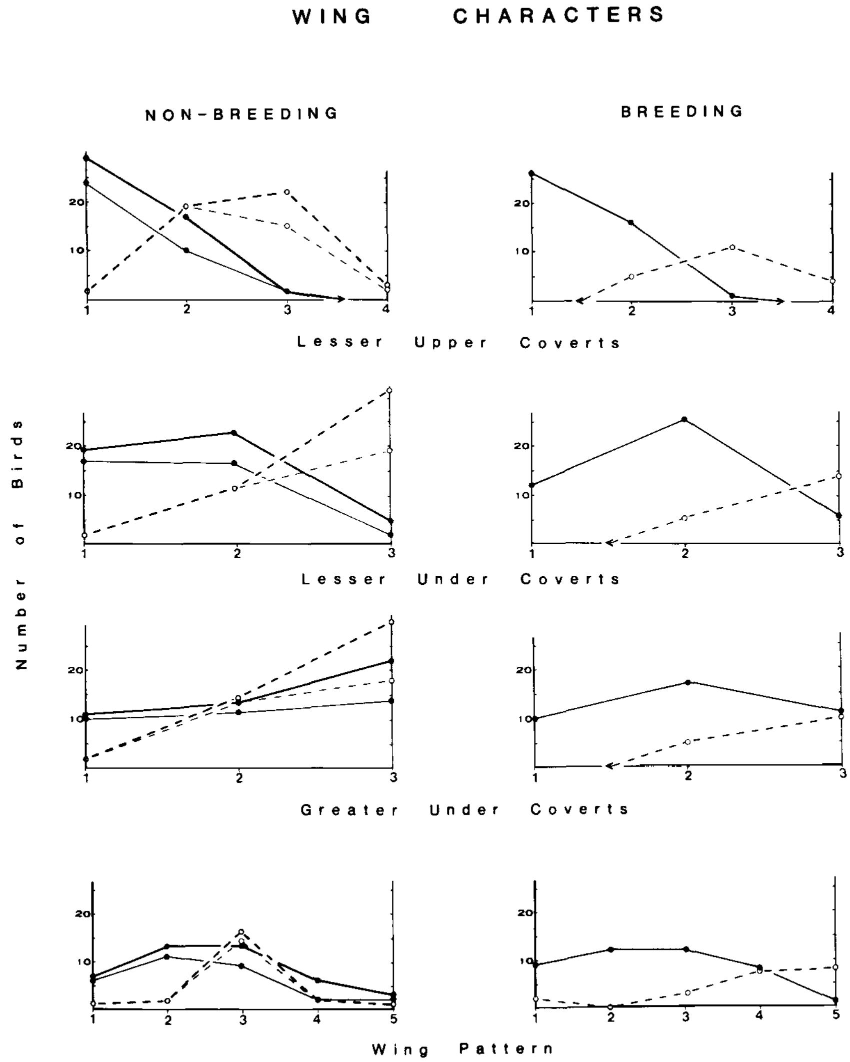

Fig. 6. Distribution of wing characters by color phase and season. For explanation of symbols and lines, see legend to Fig. 4.

greatly and there was complete overlap between the phases, birds of both phases being found in each category. While there was a tendency for dark birds to have less and light birds more white in the wing, the median category (3) contained 31% of the dark birds and 30% of the light ones.

SKELETAL MEASUREMENTS—HERMAN SERIES

Comparison of the measurements of the leg bones and phalanges showed no significant differences between birds of the two color phases (Table 4). In addition, the ratios of the lengths of the toes to that of the tarsometatarsus did not differ significantly between the sexes.

The differences in ulna length between birds of the two phases was highly significant (*t*-test, $P < 0.01$) in both sexes. This confirms the difference in wing measurements made from freshly thawed birds (Table 3).

On the other hand, the length of the maxilla from the anterior edge of the nostril measured on the skull did not differ as significantly as did the bill-from-nostril measurement on freshly thawed birds (Table 3). Because of the

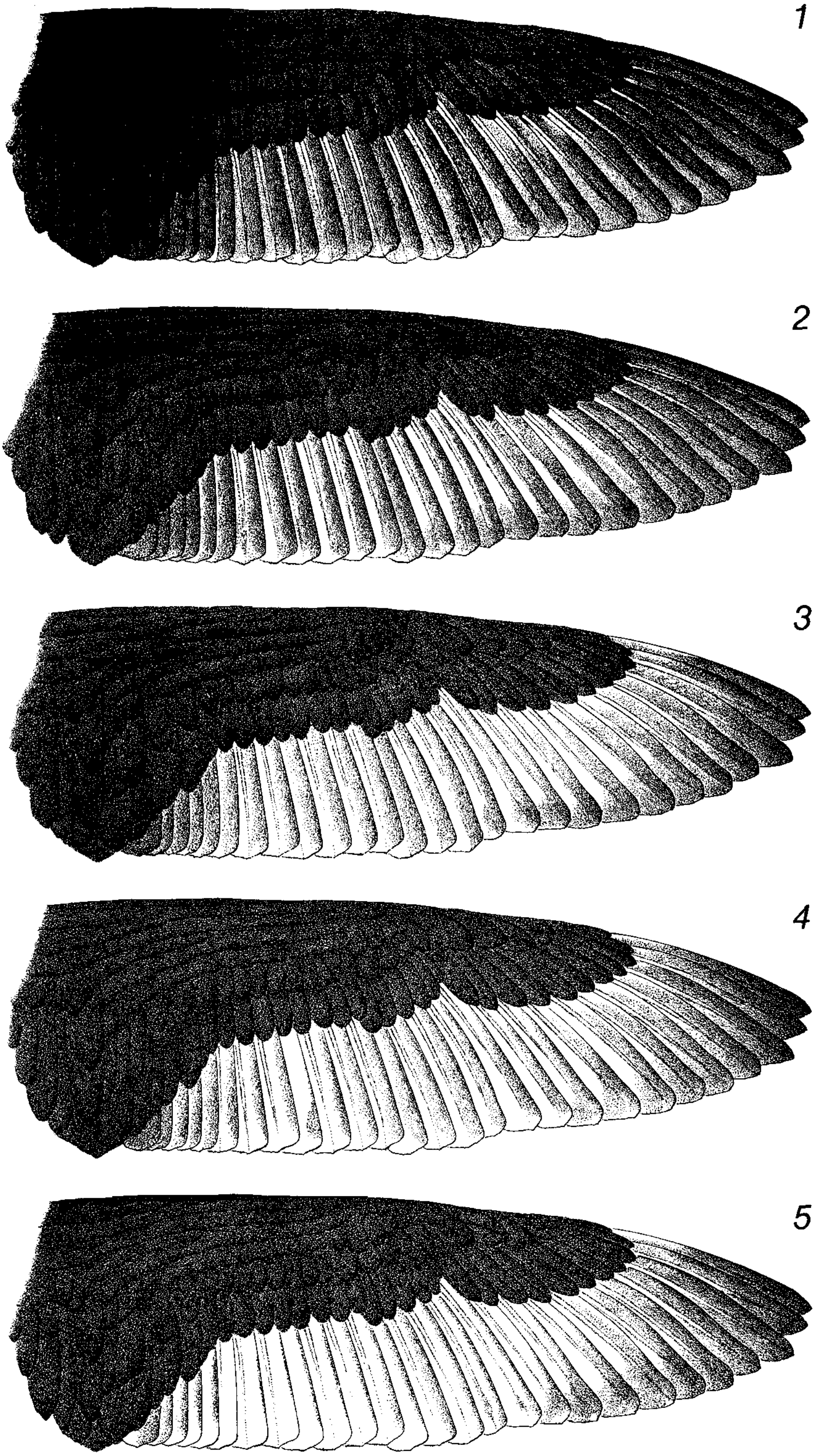

Fig. 7. Wing patterns of reference series of Western Grebes.

continual growth and wear of the rhamphotheca, the former measurement is probably the more precise.

OTHER MUSEUM SPECIMENS

Data on color patterns collected by Storer from study skins in various museums and from wings saved with the skeletons from Lake Newell, Alberta were also analyzed and compared with the Clear Lake results. The data from museum study skins agreed with those from the Herman series in showing a lesser degree of intermediacy in facial characters between the phases in breeding adults than in immature and winter birds (Fig. 2).

The color phase of the Lake Newell birds was not determined, but because the Canadian populations consist of approximately 99% dark-phase birds, we compared the Lake Newell birds only with the dark birds from Clear Lake. In the wing pattern and all three characters of the coverts, the Lake Newell birds showed more white on the average than the Clear Lake birds. We attribute much of this difference to the fact that immature birds tend to have more white in these areas than adults (Table 5). The Lake Newell sample is strongly biased in favor of immatures (94 to 23), whereas the opposite is true for the Clear Lake birds (12 to 79). In both samples there are relatively more immatures in the lighter categories than in the darker ones.

Nearly one fourth (22%) of the Lake Newell sample had a white patch on or near the leading edge of the wing. This was the result of white on the outer web of one or more of the outer primaries. This extended from the base of the feather well beyond the tips of the primary coverts and was separated from the white of the inner primaries and secondaries by the black of the primaries between. The white patch involved one (12 birds), two (6), three (7), or four (1) primaries, beginning with either the outer or next primary.

DISCUSSION AND CONCLUSIONS

The picture of the molt cycle shown by the Herman sample is somewhat blurred by the extended breeding season on Clear Lake. Even so, the general pattern presented by Palmer (1962: 95) appears to be correct in that there is an obvious concentration of the molt of all areas from July through September and a second molt, largely confined to the head, from March to May. The face patterns of light- and dark-phase birds show virtually no overlap in the breeding season, but there is a tendency for intermediacy or overlap in these characters in winter and in immature birds. This is consistent with the evidence for a partial prenuptial molt.

Given that preferential mating occurs within phases, selection would be expected to favor individuals having a breeding plumage pattern that is nonambiguous with respect to color-phase type. Of the differences in plumage color that we studied in birds of the two color phases, only the facial characters and flank pattern are readily apparent in the living bird. The importance of eye contact in courtship displays (Nuechterlein and Storer 1982) indicates that facial differences might be the most effective visual characters for this purpose. These characters show virtually no overlap during the breeding season.

In contrast to facial characters, there is considerable overlap between the phases in all other characters. Of these, only the flank pattern is ordinarily visible and therefore subject to selective pressure for divergence. The variation in the flank pattern, while showing overlap in overall darkness or lightness, is subject to great individual variation in the pattern of spots, which may result from selection favoring differences that permit individual recognition by the birds.

The feathers of the flanks, humeral tracts, interscapular tracts, and base of the legs appear to undergo molt almost continuously. At least in the case of the flanks, this situation appears to be the rule in grebes. This continuous molt makes possible the ingestion of feathers throughout the year. We have seen no behavior indicating that feathers are actually plucked by the grebes; instead, the feathers swallowed appear to be those that are lost naturally during preening. Frequent preening of this area and subsequent feather loss may possibly stimulate molt. In any case, the constant molt and regrowth of feathers for use in the stomach is probably unique to grebes.

The wide variation in the wing patterns of Western Grebes contrasts with the relatively fixed wing patterns found in many water birds. Selection for a fixed, species-specific pattern probably is not strong in Western Grebes because these birds migrate at night, rarely fly at

TABLE 4. Skeletal measurements (mm) from Clear Lake birds by sex and color phase.

	Dark females		Light females		Dark males		Light males	
	n	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)
Femur								
Length	11	43.16 (1.45)	10	42.70 (1.82)	16	47.16 (1.63)	15	46.27 (1.76)
Prox. width	12	13.23 (0.48)	11	13.46 (0.70)	16	14.69 (0.66)	17	14.41 (0.47)
Shaft width	12	5.20 (0.20)	11	5.20 (0.31)	16	5.69 (0.28)	15	5.54 (0.18)
Dist. width	11	14.05 (0.40)	11	14.08 (0.62)	16	15.36 (0.50)	17	15.19 (0.54)
Patella								
Length	12	20.10 (1.28)	11	19.53 (1.69)	16	21.46 (1.28)	17	21.55 (1.20)
Width	12	8.97 (0.37)	11	8.80 (0.67)	16	9.60 (0.58)	16	9.44 (0.52)
Tibiotarsus								
Length	12	133.27 (2.78)	9	133.87 (5.55)	16	143.84 (5.45)	13	142.75 (3.91)
1 to artic.	12	113.67 (2.61)	9	114.04 (3.95)	16	123.36 (4.52)	15	122.05 (3.43)
1 crest	11	19.59 (0.74)	11	19.76 (1.59)	12	20.79 (1.88)	15	20.81 (0.90)
Prox. width	12	9.97 (0.30)	11	10.03 (0.41)	16	10.90 (0.29)	17	10.78 (0.37)
Shaft width	12	5.53 (0.30)	11	5.70 (0.31)	16	6.17 (0.24)	17	6.05 (0.22)
Dist. width	12	10.11 (0.38)	11	10.18 (0.61)	16	11.15 (0.30)	17	11.09 (0.41)
Tarsometatarsus								
Length	12	71.68 (1.94)	11	72.11 (2.20)	16	77.21 (2.73)	17	77.43 (2.56)
Prox. width	12	12.13 (0.38)	11	12.31 (0.74)	16	13.40 (0.30)	17	13.38 (0.45)
Shaft width	12	3.38 (0.18)	11	3.25 (0.39)	16	3.67 (0.26)	17	3.59 (0.15)
Dist. width	12	8.08 (0.32)	11	8.11 (0.48)	16	8.91 (0.34)	17	8.86 (0.23)
Digit I	7	11.86 (0.74)	11	12.32 (0.56)	15	12.38 (0.92)	14	12.59 (0.67)
Digit II								
Phalanx 1	12	25.23 (0.92)	11	25.42 (0.95)	16	26.73 (1.14)	17	26.54 (0.87)
Phalanx 2	12	23.80 (0.96)	11	24.53 (1.29)	16	26.08 (0.97)	17	25.98 (0.66)
Digit III								
Phalanx 1	12	24.28 (0.92)	11	24.68 (1.08)	16	25.94 (1.15)	17	25.91 (0.76)
Phalanx 2	12	18.01 (0.61)	11	17.92 (0.76)	16	18.83 (0.69)	17	18.92 (0.65)
Phalanx 3	12	17.41 (0.62)	11	17.67 (0.95)	16	18.82 (0.82)	17	18.88 (0.71)
Digit IV								
Phalanx 1	12	27.94 (1.22)	11	28.36 (1.23)	16	29.88 (1.57)	17	30.05 (1.00)
Phalanx 2	12	13.51 (0.51)	11	13.44 (0.67)	15	14.03 (0.49)	17	14.29 (0.51)
Phalanx 3	12	12.91 (0.76)	11	13.00 (0.51)	15	13.55 (0.67)	17	13.30 (0.57)
Phalanx 4	11	14.73 (0.77)	11	14.82 (0.85)	16	15.74 (0.78)	17	15.82 (0.50)
Digit II								
Total length	12	49.03 (1.80)	11	49.95 (2.12)	16	52.80 (2.04)	17	52.52 (1.44)
Digit III								
Total length	12	59.70 (1.96)	11	60.27 (2.66)	16	63.58 (2.47)	17	63.71 (1.74)
Digit IV								
Total length	11	69.08 (2.90)	11	69.61 (2.91)	15	73.02 (2.97)	17	73.46 (2.03)
Digit I/TTL[a]	12	0.76 (0.002)	9	0.76 (0.004)	16	0.77 (0.003)	13	0.77 (0.003)
Digit II/TTL	12	0.38 (0.007)	9	0.38 (0.012)	16	0.37 (0.011)	13	0.37 (0.006)
Digit III/TTL	12	0.45 (0.010)	9	0.45 (0.015)	16	0.44 (0.013)	13	0.45 (0.012)
Digit IV/TTL	11	0.52 (0.018)	9	0.52 (0.018)	15	0.51 (0.015)	13	0.52 (0.013)
Ulna								
Length	23	101.37 (3.27)	13	98.39 (1.86)	38	109.45 (3.36)	18	106.19 (3.37)
Bill (skeleton)	20	40.74 (2.08)	12	39.60 (2.89)	41	48.73 (2.89)	18	46.40 (2.92)

[a] TTL = length of tibiotarsus.

other times, and otherwise show the wing pattern only during wing stretching, a comfort movement with no known social function. The winter sample shows more intermediacy than the sample taken in the breeding season. Dark juveniles tend to have more and light juveniles less white in the wings than adults. Whether juveniles acquire different wing patterns after their first wing molt or whether this apparent difference results from the small sample size

TABLE 5. Wing characters of Clear Lake and Lake Newell birds by age.

		Clear Lake		Lake Newell	
Character	State	Adult (%)	Immature (%)	Adult (%)	Immature (%)
Lesser upper coverts	1	50 (63)	5 (42)	6 (26)	39 (42)
	2	26 (33)	7 (58)	12 (52)	50 (54)
	3	3 (30)	0 (0)	5 (22)	4 (9)
	Total	79	12	23	93
Lesser under coverts	1	29 (37)	2 (18)	3 (14)	3 (3)
	2	41 (53)	6 (55)	19 (86)	60 (67)
	3	8 (10)	3 (37)	0 (0)	26 (26)
	Total	78	11	22	89
Greater under coverts	1	20 (26)	1 (9)	2 (9)	1 (1)
	2	28 (36)	2 (18)	10 (43)	6 (6)
	3	30 (38)	8 (73)	11 (48)	86 (93)
	Total	78	11	23	93
Wing pattern	1	15 (21)	1 (8)	5 (22)	3 (3)
	2	23 (32)	2 (17)	13 (57)	16 (17)
	3	21 (20)	4 (33)	3 (13)	37 (40)
	4	10 (14)	4 (33)	2 (9)	32 (34)
	5	3 (4)	1 (8)	0 (0)	5 (5)
	Total	72	12	23	93

remains to be determined. Some birds of unknown age molt their remiges in midwinter.

The morphological differences between light- and dark-phase birds on Clear Lake, California correspond closely to those between the birds of the southern United States and the more northern populations, respectively. The clinal increase in wing length without a parallel change in tarsal length indicates a relatively longer wing in the north, which presumably is related to the extensive migrations undertaken by the northern birds. The differences in the birds of the two color phases on Clear Lake may be the result of colonization of this lake by dark-phase northern birds. If the dark-phase birds of the Clear Lake population colonized the lake from the north, the morphological differences between birds of the two phases may not be representative of the species as a whole.

In a sample of 40 birds from the Bear River marshes, Utah that was evenly divided between males and females and between dark- and light-phase birds, Ratti et al. (1983) found the length of bill from nostril was significantly greater in dark-phase birds of both sexes. Wings were longer, but not significantly so, in dark-phase birds of both sexes. Total culmen length and bill depth were significantly greater in females of the dark phase. Even at Bear River, the birds nest in an artificially maintained habitat, and therefore the population may not be suitable for analyzing possible differences between the phases in a population where the two have been coexisting for a long period.

Lawrence (1950: 11) found that centrarchid fishes comprised the major part of the diet of Western Grebes on Clear Lake, but he did not analyze his data on food habits by sex or color phase. Feerer (1977: 84–87) examined stomach contents of the Herman sample from Clear and Topaz lakes and found centrarchids in 25 of the 31 stomachs containing identifiable prey, cyprinid fishes in 8, and crayfish in 2. The male grebes in this sample had ingested "significantly larger fish ($P < 0.01$) than female Western Grebes." This difference between the sexes in food habits is to be expected because of the sexual dimorphism, especially in the size of the bill. Feerer also found that stomachs from light-phase females contained "significantly smaller fish ($P < 0.05$)" than dark-phase females, although he found no significant differences between males of the two groups.

Nuechterlein (1981: 343–344) pointed out that light-phase birds tend to use "springing dives" (Lawrence 1950) more frequently than "level dives" and suspected that this was a result of their going deeper, which in turn resulted from "spatial segregation of the morphs during feeding." Light-phase birds generally tended to feed further from shore than dark-phase birds. These observations suggested possible adaptations for foraging at different depths, but analysis of measurements of the leg and toe bones (Table 4) indicates that there are no significant differences in size or proportion of the hind limb between birds of the two color phases. Thus no osteological differences have evolved in the leg to accompany this apparent behavioral difference.

A thorough study of the comparative ecology of birds of the two color phases of the Western Grebe has yet to be undertaken on a body of water that has not been considerably altered by man. The levels of Clear and Topaz lakes and of the Bear River marshes are artificially controlled. The widespread use of pesticides containing chlorinated hydrocarbons caused a disastrous decline in the Western Grebe population on Clear Lake and, presumably, other serious changes in the ecology of the lake. Most of the centrarchids taken by Western Grebes on Clear Lake [bluegills (*Lepomis macrochirus*), crappies (*Pomoxis* spp.), and largemouth bass (*Micropterus salmoides*)] are introduced, as is the carp (*Cyprinus carpio*), the most frequent prey of the grebe at the Bear River marshes (Lindvall 1976: 50). Introduction of exotic aquatic plants and destruction of plants by introduced fishes can radically alter habitats by increasing the turbidity of the water and altering the kinds, sizes, and shapes of available prey. Such factors could affect, and probably have affected, the balance between birds of the two color phases in the areas where they have been studied most intensively. For this reason, conclusions as to the comparative ecology of these birds must be regarded as tentative.

Intermediates in the facial pattern between the phases apparently are rare among breeding birds collected north of Mexico. Intermediacy is expressed almost entirely in the winter plumage. Ratti (1979: 575) suggests that "whitish lores on dark-phase birds are associated with winter plumage and the lores may darken in breeding plumage." Our evidence from the Herman series and from museum skins supports this idea and indicates that many of these "intermediates" are first-year birds. Feerer (1977: 83) listed nine birds "intermediate" between the two phases in plumage. He determined four of these to be immatures on the basis of the presence of down in the plumage. We received four of the remaining five, all of which had incompletely fused tarsometatarsi and hence were young birds. The fifth bird, collected 2 May 1968 on Clear Lake, had testes measuring 13 × 8 mm and 11 × 7 mm, considerably smaller than those of other males collected on that date. Thus, it is likely that this bird was hatched late in 1967 and had not attained full nuptial plumage by the time it was collected.

Feerer (1977) suggests that "significant clinal distributions in latitude and mean air temperature indicate that Western Grebe forms have a different climatic preference." Yet there are important exceptions to this clinal distribution hypothesis (Feerer 1977, Ratti 1979), and the possible selective factors favoring the different patterns of dark and light in the plumage have not been studied. The longer retention of white down by light-phase young as compared to their dark-phase counterparts (Ratti 1979) may be related to the prevention of heat stress through reflection of solar radiation. A similar argument might be made for the more extensive light edging of the back feathers of adult light-phase birds. Finally, differences in the amount of light and dark in the flanks might possibly be related to differences in the optimal pattern of countershading while diving at different water depths. These speculations might merit investigation.

The Western Grebe (*sensu lato*) represents a seldom documented stage in the speciation process. Both color phases occur sympatrically throughout the range of the species, and geographic variation in size occurs independently of phases. This parallel variation in size indicates that if the phases evolved as allopatric populations, their ranges merged completely before the behavioral isolating mechanisms developed or became effective. There is some evidence that males with an intermediate facial pattern experience difficulty in finding mates (Nuechterlein 1981), but this needs further documentation. The preponderance of dark-phase birds in the northern part of the species range and the longer wings of the northern birds are evidence that dark-phase birds may have arisen in the north when the species was divided [perhaps, as Feerer (1977: 62–66) suggested, during a period of arid climate when habitats at intermediate latitudes were absent] and that it subsequently merged with the smaller, light-phase birds to the south. [Feerer's (1977: 66) citing of "evidence of non-overlap of morphological characters of light-form and dark-form Western Grebes in Mexico

(Dickerman 1973) stemmed from a misinterpretation of Dickerman's table, in which Dickerman used *clarkii* for the whole Mexican population and *occidentalis* for those in the United States and Canada, rather than for the color phases.]

Before the merging of the populations, the Advertising call differences (Nuechterlein 1981) may have arisen in the two populations but with incompletely specific response to each. Thus, early in the merging process, differences in size presumably became fixed, and color characters not involving the face became mixed (if there was segregation of these characters in the period of isolation) within the various populations through extensive interbreeding between birds of the two phases. At present, reproductive isolation between the phases may be increasing, and with it the completion of the speciation process. Regardless of whether or not the forms arose in allopatry, it appears that the later stages of the process are occurring in sympatry. With speciation accomplished, selection can be expected to favor ecological differences, such as those Feerer and Nuechterlein have suggested, to become accentuated, and with them, morphological differences.

Taxonomic considerations.—From the recent studies of Feerer (1977), Ratti (1979), and Nuechterlein (1981), it is evident that in the Western Grebe populations in Utah and California a high degree of assortative mating occurs and that this is largely based on behavioral isolating mechanisms. Yet mixed pairs and birds of intermediate facial plumage are known to produce viable young (Nuechterlein unpubl. data), and males of the two phases frequently join in mutual courtship displays (Nuechterlein 1981). One important isolating mechanism is a difference in the number of notes in the Advertising call, which is used to attract mates. Were such assortative mating the rule throughout the range of the Western Grebe, the two phases could be said to have reached the level of species. However, in the northern part of the range, where the light-phase birds are rare, the phase-specific response to Advertising calls is lowered (Nuechterlein 1981), and in Mexico there appear to be many intermediates. Because breeding in Mexico often is nonseasonal, it is not clear whether these are young, birds in winter plumage, or hybrids. If the last is the case, we think the two forms may better be treated as color morphs.

A further complicating factor is that all birds of the Mexican population are distinctly smaller than those of the rest of the species' range. Thus, if the two phases are considered species, the dark-phase Mexican birds and the light-phase northern birds will require subspecific names. We prefer the conservative treatment, that is, to recognize the two phases as species if and when the color phases in the Mexican population are shown to be reproductively isolated from each other. In either case, it is the situation, not the nomenclature (or the potential length of life lists), that is of prime biological interest. We know of no other similar situation.

ACKNOWLEDGMENTS

The gift of the large series of frozen Western Grebes through Steven G. Herman to the UMMZ both provided the impetus for this paper and made it possible. We are also greatly endebted to Drs. Herman and Robert L. Rudd for information about the birds and the lakes on which they were taken, as well as to Dr. Robert W. Nero for the gift of the Lake Newell birds to this museum. Jean W. Cohn, Steven M. Goodman, Janet G. Hinshaw, Douglas A. Nelson, Jill M. Trainer, and Marina A. Wong assisted in the important task of preparing the birds as pelts and skeletons. Margaret Van Bolt prepared Figures 1 and 7 and gave helpful advice on the preparation of the other figures. The manuscript was read by Steven M. Goodman, Joseph R. Jehl, Jr., Robert S. Voss, Ned K. Johnson, John T. Ratti, and an anonymous reviewer, all of whom we wish to thank for their helpful comments.

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APPENDIX. Western Grebe color character states and reference specimens from The University of Michigan Museum of Zoology (UMMZ).

Character	State	UMMZ number
Position of dark-white border	1—Below eye	No reference specimens
	2—Intersects eye	
	3—Above eye	
Color over eye	1—Black	No reference specimens
	2—White	
Extent of color behind eye	1—All dark	204,475
	2	204,574
	3	204,478
	4	204,530
	5—All white	204,476
Extent of color below eye	1—Much	204,475
	2	204,574
	3	204,478
	4	204,477
	5	204,459
	6—None	204,476
Color of lores	1—Dark gray	204,475
	2—Light gray	204,477
	3—White	204,468
Mottling of lores	1—Unmottled	None
	2—Mottled	204,459
Base of crest	1—Dark gray	204,475
	2—Light gray	204,477
	3—Mottled	204,476
	4—White	204,468
White bases to scapular coverts	1—None	204,558
	2—Little	204,550
	3—Moderate	204,473
	4—Much	204,485
Flank pattern	1—Solid dark	204,553
	2	204,551
	3	204,552
	4	204,469
	5	204,476
	6	204,468
	7—Small dark spots	204,485
White bases to lesser upper wing coverts	1—No white	204,554
	2—Small centers	204,552
	3—Medium centers	204,473
	4—Large centers	204,469
Lesser under wing coverts	1—Heavy dark edges	204,554
	2—Thin dark edges	204,551
	3—All white	204,485
Greater under wing coverts	1—Gray	204,558
	2—Speckled	204,553
	3—White	204,485
Wing pattern	1—Darkest	204,558
	2	204,554
	3	204,551
	4	204,548
	5—Lightest	204,485

SEASONAL CHANGES IN THE HABITAT DISTRIBUTION OF TRANSIENT INSECTIVOROUS BIRDS IN SOUTHEASTERN ARIZONA: COMPETITION MEDIATED?

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ABSTRACT.—The distribution and abundance of 26 migratory insectivorous bird species were recorded over an elevational habitat gradient in the Chiricahua Mountains, Arizona for the spring and fall migratory seasons. Most of the species used this area only during migratory passage, and 54% exhibited significant shifts in the habitats occupied from spring to fall. The majority (69%) of species also exhibited significant changes in density within habitats between seasons. Using pairwise correlations of bird densities from 7 habitat types and 2 seasons, I identified 5 groups that contained species whose seasonal distributional patterns were similar to one another but independent and distinct from members of the other 4 groups. Despite independence among groups in the seasonal patterns of habitat distribution, the combined density of all species was significantly positively correlated with a measure of food availability taken from each of the habitat types in each migratory season. Consequently, the spring-to-fall change in insect density within each habitat also was significantly correlated with the seasonal change in bird density over each of the habitat types. The hypotheses that best explain these correlations include that in which competitive adjustments among the migratory birds enable a close match to food resource availability and that whereby noncompetitive adjustments occur in response to the diversity (itself correlated with food abundance) of food types available. *Received 7 May 1984, accepted 18 August 1984.*

EXPLANATIONS for patterns in bird community structure routinely have been sought from knowledge of food resource distributions and abundances (MacArthur 1969, 1970, 1972; Cody 1974). This stems logically from the idea that natural selection should lead toward the utilization of currently underutilized resources, and competition among species should determine both the number and relative abundance of species that use those food resources. More recently, however, Wiens (1977, 1983) suggested that the match between resource levels and species utilization patterns will be less than perfect because unpredictability or instability in resource levels cannot be tracked rapidly enough by bird populations (but see Cody 1981). In fact, recent experimental evidence (Emlen 1978, 1979, 1981; Emlen and DeJong 1981) suggests that birds are rather fixed in their foraging behaviors and that a close tracking of resource levels is impossible. This means that, except for the occasional year of an ecological crunch when resources are scarce, many aspects of community structure would result as much from stochastic processes as from deterministic ones (Wiens 1977, 1981; Rotenberry and Wiens 1980a, b).

Although most of the discussion and uncertainty about the role of food resource levels in controlling bird community composition revolves around breeding populations, a unique situation for testing whether birds respond, in an ultimate sense, to seasonal changes in food levels exists with migratory birds. Changes in vegetation structure and food resource levels from spring to fall are not of equal magnitude among habitat types. This provides the opportunity to ask whether bird community structure changes in response to changes in the distribution of food resources.

In this paper I outline the patterns of habitat use by small, insectivorous bird species of southeastern Arizona during both migratory seasons and test whether the habitat distribution of these birds is independent of migratory season. This is followed by an analysis of the relationships between bird densities and various habitat parameters, including food availability. If interspecific and intraspecific competition for food are important during the migratory seasons, then the combined density of similar-sized, insectivorous birds would be expected to match the relative food resource levels among habitats within a season and, therefore, to match any seasonal changes in relative food levels among habitats. If food is of little ultimate importance in determining bird community composition, or if food levels are important but changes in food levels are impossible to track closely, then independence between bird densities and food densities would be expected.

STUDY AREA AND METHODS

I conducted bird censuses and recorded vegetation parameters and insect densities in each of 7 homogeneous habitat types in the Chiricahua Mountains, Arizona (Fig. 1). The 7 sites occurred along an elevational gradient and ranged from low and simple to tall and complex in vegetation structure. The first site (desert flat) was located 2 km northeast of Portal (31°55′N, 109°07′W) at an elevation of 1,402 m and was dominated by desert scrub vegetation, including *Acacia constricta, Larrea tridentata, Chilopsis linearis,* and *Prosopis juliflora.* The second site (desert wash) was located along lower Cave Creek 2 km northeast of Portal (31°55′N, 109°07′W) at an elevation of 1,433 m and contained many of the vegetation elements that characterized the desert flats plus scattered *Platanus wrightii* and dense sections of *Fallugia paradoxa* and *Chrysothamnus nauseosus.* The third site (creek bottom) was located along the south fork of Cave Creek 7 km southwest of Portal (31°52′N, 109°11′W) at an elevation of 1,631 m; this site was dominated by *Pinus ponderosa, Quercus arizonica, Q. hypoleucoides,* and *Picea engelmanni.* The fourth site (pine-oak woodland) was located behind the American Museum's Southwestern Research Station 7 km southwest of Portal (31°53′N, 109°12′W) at an elevation of 1,676 m and was dominated by *Pinus leucophylla, Quercus emoryi, Q. arizonica,* and *Juniperus deppeana.* The fifth site (pine-oak-juniper woodland) was located 12 km west of Portal (31°57′N, 109°16′W) at an elevation of 2,286 m and was dominated by the same vegetation elements as the pine-oak woodland, plus *Pinus cembroides, P. ponderosa,* and *Quercus gambelii.* The sixth site (pine forest) was located at the turnoff to Barfoot Park 12 km west of Portal (31°55′N, 109°16′W) at an elevation of 2,512 m and was dominated by *Pinus ponderosa.* The last site (pine-fir forest) was located at Rustler Park 13 km west of Portal (31°54′N, 109°17′W) at an elevation of 2,682 m and was dominated by *Abies concolor, Picea engelmanni, Pseudotsuga menzeisii, Pinus ponderosa,* and *P. strobiformis.*

Bird censuses.—I censused birds in each site by walking a 1-km line transect beginning at daybreak and recording birds detected by sight or sound within a fixed width that varied from 25 to 30 m, depending upon the habitat involved. The fixed-width transect method provides bird density estimates that are thought to be quite reliable relative to other commonly employed transect census techniques (Amman and Baldwin 1960, Robinette et al. 1974, Franzreb 1981, Tilghman and Rusch 1981). At least 4 censuses were conducted in each site during each season (a number deemed adequate for comparative work; Anderson and Ohmart 1977). For each site the 1975 censuses were combined with 1978 censuses for the fall sample. In all but 2 cases, a single 1975 census was combined with 3 or more 1978 censuses. In the 2 exceptions (desert flats and pine-oak woodlands), 2 censuses were conducted in 1975 and the rest in 1978. Because the distribution of bird densities among species did not differ between years (ANOVAs, $P > 0.05$), I feel that combining fall census data from the two years is justified.

Although the same census route within a site was used each time, for statistical purposes I treated each census as an independent estimate of the bird density in a given habitat because (1) stopover periods for transients (the large majority of birds in this study; see Results) rarely exceeded 4–6 days (unpubl. banding records) and (2) successive censuses in a given habitat were spaced at least one week apart due to the rotation of censuses among sites.

For the purposes of this report I have restricted my analyses and discussion to the small, insectivorous, foliage-gleaning bird species that belong to the families Remizidae, Aegithalidae, Muscicapidae (Sylviinae only), Vireonidae, and Emberizidae (Parulinae only; A.O.U. 1983).

Bird residence status.—A bird species was classified as transient in a given study site if it could be found there only during one or both migratory seasons. The breeding status of each species in each site was determined from breeding census data provided by Balda (1967), M. Cody (pers. comm.), and K. Garrett (pers. comm.), each of whom conducted censuses close to, if not precisely within, my study sites.

Vegetation measurements.—I measured some vegetation parameters that have been shown through previous work (James 1971, Whitmore 1975) to be important in distinguishing bird species that co-occur within a restricted geographic location. On a single occasion in each site during the fall of 1975 and the spring of 1976, I counted the number of times foliage hit an extendable pole that was raised through the vegetation at 100 points (1 every 10 m) 5 m to one side of the census route, alternating left and right from one point to the next. An imaginary extension for taller habitats was provided by a camera and telephoto lens. I used the total number of hits as an estimate of vegetation density (VEGTOT), the total number of hits from ground level to 1 m as an estimate of understory density (VEGONE), the proportion of points that contained at least 1 hit at >5 m as an estimate of canopy cover (CANCOV), the number of perennial plant species hit as an estimate of plant species richness (PSRICH), and the maximum vegetation height at each point averaged over all points as an estimate of mean vegetation height (HEIGHT).

Three vegetation variables were statistically significantly ($P < 0.05$) intercorrelated: VEGTOT with CANCOV ($r = 0.78$), VEGTOT with HEIGHT ($r = 0.74$), and CANCOV with HEIGHT ($r = 0.96$). I retained all variables in my analyses, however, because they were different enough to reveal differences in the significance of their correlations with bird density. None of the vegetation variables was significantly correlated with the index of insect abundance (defined below).

Food availability.—I did not attempt to sample the same prey species that foliage-gleaning insectivores capture. Even samples that include only prey species captured by the birds would not be immune from criticism that the prey cannot be captured in the same manner that birds capture them and, therefore, that such samples still might fail to provide an accurate measure of food availability. Instead, I used a more general sampling scheme (below) and made the assumption that the calculated values were correlated with actual prey availability.

Prey availability was estimated from counts of flying insects caught on 10 × 10-cm plastic squares coated with Tanglefoot® that were hung in vegetation at 0.5-m height intervals to 2.0 m [see Hutto (1980) for discussion of the efficacy of this method]. At each site and in each season (1975 and 1976), 20 boards (5 stations with 4 boards each, every 200 m along the transect route) were left hanging for 24 h before I counted the insects. The boards were hung in precisely the same spots in both seasons. The number of insects captured per board is in itself an insufficient estimate of prey availability to foliage-gleaners in different habitats, unless differences in vegetation density (foraging-substrate availability) are taken into consideration. Assuming independence of insects captured and vegetation density between habitats, I calculated a relative index of the number of available insects/unit volume of vegetation (ADJINS) by multiplying the number of insects captured/site times a measure of vegetation density (VEGTOT/100) within the site. The assumption that insect abundance is independent of vegetation density is reasonable if different habitats are involved. For example, a juniper woodland of the same vegetation density as an oak woodland would have many fewer insects available to birds (Balda 1967). This assumption also is directly supported by a lack of correlation between the unadjusted index of insect abundance (as determined from sticky board samples) and either VEGONE ($r = 0.23$, NS) or VEGTOT ($r = -0.35$, NS).

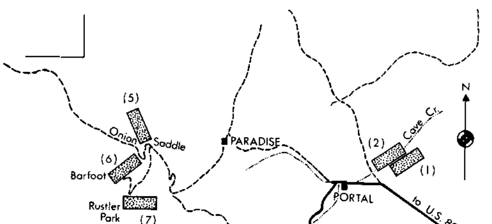

Fig. 1. Locations of the 7 study sites in the Chiricahua Mountains, southeastern Arizona. (1) Desert flat, (2) desert wash, (3) creek bottom, (4) pine-oak woodland, (5) pine-oak-juniper woodland, (6) pine forest, (7) pine-fir forest.

Results

A total of 26 small, insectivorous, foliage-gleaning bird species was recorded from the spring and fall migration-period censuses (Table 1). With the exception of the creek-bottom habitat, the number of bird species in each of the habitat types was greater in the fall than in the spring. The greatest number of species (16) was recorded during both spring and fall in the creek-bottom habitat and during the fall in the pine-fir forest.

Within a given site in either season, an average of 55% of all bird species of concern was wholly transient; that is, these species were found in these sites only during spring or fall migration. This average is conservative because an unknown proportion of individuals of some species were considered summer residents when, in fact, they were transient individuals that bred farther north than the Chiricahua Mountains. For example, one can be confident that some (or most) of the Black-throated Gray Warblers (*Dendroica nigrescens*) sighted in the creek bottom during spring were transients, but because the species is known to breed in that site, I (conservatively) called them all residents. It probably is reasonable to assume that 70–80% of the species or individuals in a given site during either spring or fall were transient, but the only certainty is that the proportion exceeded 55%. The bulk of individuals that contributed to the patterns described in this

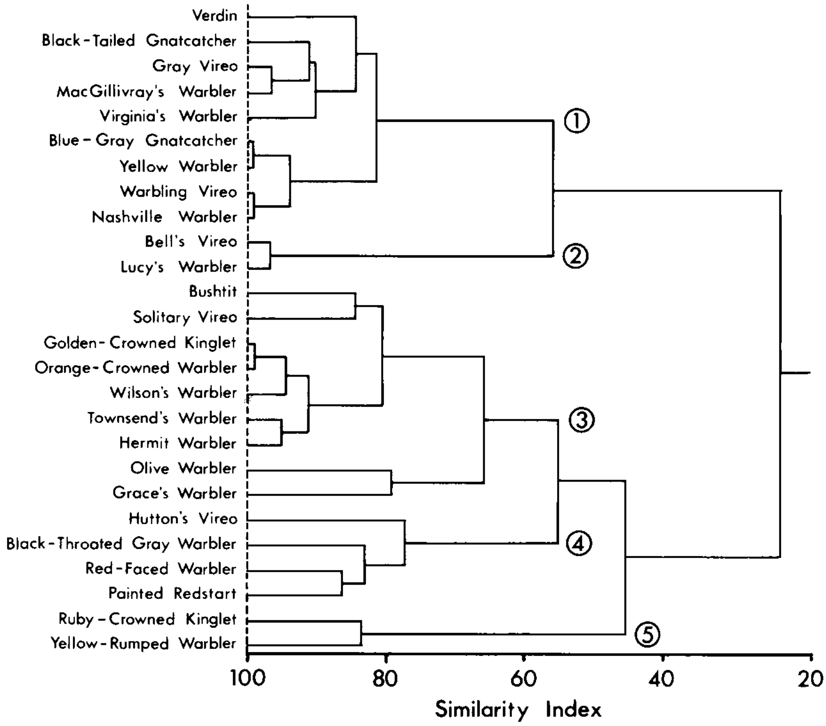

Fig. 2. Cluster dendrogram based on similarities in the seasonal distributions of 26 bird species. The 5 groups of species referred to in the text are indicated numerically.

paper are, therefore, transient species, although the analyses include resident species as well.

There was a significant (ANOVA, season × habitat; $F = 2.7$, $P < 0.05$) shift in the occupancy of the various habitat types from spring to fall, as evidenced by the combined bird densities; birds were relatively more abundant in desert flats and, especially, pine-fir forest in the fall relative to the spring (Table 1). Moreover, these changes in density were the result not only of significant changes in the densities of bird species that were present at a given habitat during both seasons (69% of the bird species exhibited significant changes in density between seasons), but also of some pronounced seasonal shifts in the kinds of species that used each habitat type. On average, there was over 30% turnover (defined in Table 1) in species from spring to fall in a given habitat. Considering each species separately, 14 of 26 species (54%) exhibited significant seasonal shifts in habitats occupied (ANOVAs, season × habitat; $P < 0.05$).

Rather than consider each of the 26 species separately to analyze their seasonal patterns of habitat use, I identified fewer ecological groups that contained species with similar habitat distributions in both seasons. This was done, first, by looking for correlations between the densities of all pairwise combinations of species using all habitats in both seasons. Sixty-four (20%) of the possible 325 pairwise correlations were significant ($r > 0.53$, $P < 0.05$), and only 2 of those were negative.

I next identified groups of species with similar patterns of habitat use by transforming the correlation coefficients into similarity indices (arccosine transformation) and then subjecting the similarity indices to a cluster analysis (average linkage; Hartigan 1981). At the 60% level of similarity, 5 distinct species groups emerged (Fig. 2). These appear to be biologically meaningful groups rather than groups that were merely forced into existence through the clustering procedure. The distribution and abundance patterns that characterize each group are outlined below.

Group 1.—There are 3 characteristics shared by the 9 species belonging to this group (Fig.

TABLE 1. Mean bird densities (n/10 ha) during spring (S) and fall (F) migratory periods for each of the 7 habitat types.

Species	Desert flats		Desert wash		Creek bottom		Pine-oak		Pine-oak-juniper		Pine		Pine-fir	
	S	F	S	F	S	F	S	F	S	F	S	F	S	F
Verdin (*Auriparus flaviceps*)	15.0	14.3	10.1	7.7	—	—	—	—	—	—	—	—	—	—
Bushtit (*Psaltriparus minimus*)	—	—	—	1.2	4.8	11.3	2.4	22.9	1.2	29.8	—	2.4	—	17.6
Golden-crowned Kinglet (*Regulus satrapa*)	—	—	—	—	—	—	—	—	—	—	—	—	1.2	11.6
Ruby-crowned Kinglet (*R. calendula*)	0.3[a]	—	3.6[a]	—	16.0[a]	0.3[a]	5.2[a]	1.9[a]	31.6[a]	3.0[a]	17.5[a]	1.8[a]	19.1	3.7
Blue-gray Gnatcatcher (*Polioptila caerulea*)	0.3[a]	3.2[a]	—	8.3[a]	0.4	—	—	—	—	—	—	—	—	—
Black-tailed Gnatcatcher (*P. melanura*)	1.0	2.4	—	1.2	1.2	—	—	—	—	—	—	—	—	—
Bell's Vireo (*Vireo bellii*)	—	—	5.4	0.6	—	—	—	—	—	—	—	—	—	—
Gray Vireo (*V. vicinior*)	—	0.4[a]	—	—	—	—	—	—	—	—	—	—	—	—
Solitary Vireo (*V. solitarius*)	—	—	2.4[a]	1.2[a]	2.1	2.7	—	5.2	—	1.8	—	1.2	—	5.6
Hutton's Vireo (*V. huttoni*)	—	—	—	—	3.5	5.3	0.8	4.8	0.6	2.4	—	1.2	—	—
Warbling Vireo (*V. gilvus*)	—	2.8[a]	—	3.0[a]	—	1.7[a]	—	—	—	—	—	—	—	—
Orange-crowned Warbler (*Vermivora celata*)	—	0.4[a]	4.8[a]	—	0.6[a]	0.3[a]	—	—	—	1.8[a]	—	2.4[a]	—	32.9[a]
Nashville Warbler (*V. ruficapilla*)	—	1.2[a]	—	1.2[a]	—	0.3[a]	—	—	—	—	—	—	—	—
Virginia's Warbler (*V. virginiae*)	—	6.0[a]	1.8[a]	3.0[a]	3.1	0.7	—	—	—	—	—	—	—	0.5
Lucy's Warbler (*V. luciae*)	4.4	—	13.7	5.4	—	—	—	—	—	—	—	—	—	—
Yellow Warbler (*Dendroica petechia*)	—	1.2[a]	—	3.6[a]	—	0.7[a]	—	0.5[a]	—	—	—	—	—	—
Yellow-rumped Warbler (*D. coronata*)	1.0[a]	—	2.4[a]	—	0.6[a]	—	10.3[a]	1.0[a]	29.8[a]	3.6[a]	7.1[a]	9.5[a]	2.5	10.6
Black-throated Gray Warbler (*D. nigrescens*)	—	0.8[a]	—	1.8[a]	14.8	4.0	11.5	4.3	—	2.4	—	0.6[a]	—	0.9[a]
Townsend's Warbler (*D. townsendi*)	—	—	—	—	0.4[a]	1.3[a]	—	2.4[a]	0.6[a]	4.2[a]	1.6[a]	7.7[a]	3.7[a]	11.6[a]
Hermit Warbler (*D. occidentalis*)	—	—	—	—	0.6[a]	0.7[a]	0.4[a]	4.8[a]	—	2.4[a]	2.4[a]	3.6[a]	1.9[a]	12.5[a]
Grace's Warbler (*D. graciae*)	—	—	—	—	2.7	1.3	4.4	4.3	—	3.0	7.9	3.6	0.6	2.8
MacGillivray's Warbler (*Oporornis tolmiei*)	0.3[a]	18.3[a]	4.8[a]	3.6[a]	—	—	—	—	—	0.6[a]	—	—	—	3.7[a]
Wilson's Warbler (*Wilsonia pusilla*)	1.0[a]	2.0[a]	5.4[a]	2.4[a]	1.9[a]	9.3[a]	—	2.9[a]	0.6[a]	2.4[a]	—	1.2[a]	—	19.9[a]
Red-faced Warbler (*Cardellina rubrifrons*)	—	—	—	—	1.5	0.3	—	—	—	—	—	—	—	0.9
Painted Redstart (*Myioborus pictus*)	—	—	—	—	17.1	14.0	—	—	—	—	—	—	—	0.5[a]

TABLE 1. Continued.

Species	Desert flats		Desert wash		Creek bottom		Pine-oak		Pine-oak-juniper		Pine		Pine-fir	
	S	F	S	F	S	F	S	F	S	F	S	F	S	F
Olive Warbler (*Peucedramus taeniatus*)	—	—	—	—	0.2[a]	—	—	—	—	1.8	6.4	1.8	3.7	4.6
Censuses (*n*)	7	6	4	4	8	5	6	5	4	4	4	4	4	4
Total density	22.3	53.0	54.4	44.2	70.3	54.2	35.0	55.0	64.4	59.2	42.9	37.0	32.7	139.9
Species (*n*)	8	12	10	14	16	16	7	11	6	13	6	12	7	16
Species turnover[b]	50%		42%		19%		22%		37%		33%		39%	

[a] All individuals of this species in this location known to be transient.

[b] Calculated as (number of species unique to spring + number unique to fall)/(number of species present in spring + number present in fall).

TABLE 2. Values of each of 6 environmental variables recorded during spring (S) and fall (F) in each of the 7 habitat types.

Variable	Habitat type													
	Desert flat		Desert wash		Creek bottom		Pine-oak		Pine-oak-juniper		Pine		Pine-fir	
	S	F	S	F	S	F	S	F	S	F	S	F	S	F
VEGTOT	66	217	135	263	441	480	252	307	241	250	224	261	328	530
VEGONE	41	150	100	197	33	94	34	119	28	44	34	72	4	136
CANCOV	00	00	5	9	71	84	33	36	21	26	68	72	89	92
PSRICH	7	8	9	11	12	12	4	4	7	7	4	4	6	7
HEIGHT	0.7	0.7	0.8	0.8	11.6	12.1	7.0	7.0	6.4	6.7	11.3	12.0	18.9	19.0
ADJINS	66	78	113	97	243	67	40	175	55	33	9	16	10	217

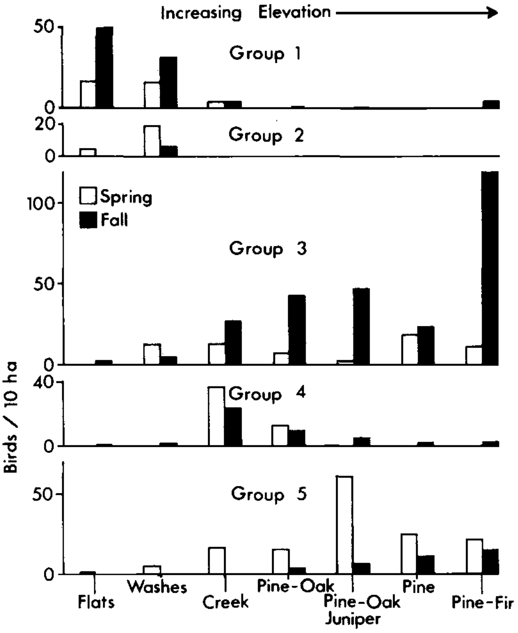

Fig. 3. Frequency histograms of the density of birds in each of 7 habitat types during spring and fall seasons. Bird species are subdivided into 5 groups, each representing a distinctive seasonal pattern of distribution and abundance. The members of each group are shown in Fig. 2.

3). They are basically desert species (ANOVA, habitat effect; $F = 18.8$, $P < 0.01$), their densities increase considerably from spring to fall (ANOVA, season effect; $F = 11.7$, $P < 0.01$), and they shift their habitat occupancy toward the desert flats in the fall (ANOVA, season × habitat; $F = 4.5$, $P < 0.01$).

Group 2.—Bell's Vireo (*Vireo bellii*) and Lucy's Warbler (*Vermivora luciae*) comprise this group (Fig. 3), and their habitat distribution is characterized by restriction to desert habitats in both seasons (ANOVA, habitat effect; $F = 16.5$, $P < 0.01$). Their densities decrease significantly from spring to fall (ANOVA, season effect; $F = 8.2$, $P < 0.01$), and they shift from desert flats and washes in the spring to exclusive use of the desert-wash habitat in the fall (ANOVA, season × habitat; $F = 4.7$, $P < 0.01$).

Group 3.—This group is composed of 9 species (Fig. 3) that are basically mid- to high-elevation birds (ANOVA, habitat effect; $F = 5.2$, $P < 0.01$) whose density increases significantly from spring to fall (ANOVA, season effect; $F = 16.4$, $P < 0.01$). These species shift markedly to the highest elevation forests in the fall (ANOVA, season × habitat; $F = 4.0$, $P < 0.01$).

Group 4.—This is principally a mid-elevation group (ANOVA, habitat effect; $F = 44.1$, $P < 0.01$) composed of 4 species (Fig. 3) whose densities decrease significantly from spring to fall (ANOVA, season effect; $F = 7.7$, $P < 0.01$). They become significantly more broad in their habitat distribution from spring to fall (ANOVA, season × habitat; $F = 2.7$, $P < 0.05$).

Group 5.—Ruby-crowned Kinglet (*Regulus calendula*) and Yellow-rumped Warbler (*Dendroica coronata*) comprise this group (Fig. 3), characterized by mid- to high-elevation birds (ANOVA, habitat effect; $F = 6.3$, $P < 0.01$) whose densities decrease significantly from spring to fall (ANOVA, season effect; $F = 17.2$, $P < 0.01$). They shift markedly from lower- to higher-elevation forests from spring to fall (ANOVA, season × habitat; $F = 3.6$, $P < 0.01$).

Thus, one can identify groups of species that use the available range of habitats during the spring and fall in a fashion that is similar to one another but differs from members of other groups. In fact, one could use a higher level of similarity from the dendrogram to identify a greater number of species groups, each distributed in distinct fashion within and between seasons, but the characteristics and biological reality of such groups become more difficult to determine.

Aspects of vegetation structure that differed greatly among sites within a season were canopy cover and mean vegetation height, while between-season changes in vegetation density and insect density generally were pronounced within a given site (Table 2). In general, the densities of birds belonging to each of the 5 species groups were well correlated with at least 1 of the vegetation parameters (Table 3). The desert groups were negatively associated with measures of tall or dense vegetation, while the birds of higher-elevation habitats were positively associated with such measures. The index of insect abundance, with one exception, was not strongly correlated with the density of any single group of birds, but it was significantly positively correlated with combined insectivorous bird density (Table 3).

Correlations between the seasonal change in magnitude of each environmental variable and the seasonal change in bird density (Table 4) show that, of the variables measured, only the

TABLE 3. Pearson product-moment correlations between environmental variables and bird densities. Each correlation was calculated with data from the 69 censuses that were conducted in the 7 habitats and 2 seasons.[a]

Group[b]	VEGTOT	VEGONE	ADJINS	CANCOV	PSRICH	HEIGHT
1	−0.31**	0.55**	−0.03	−0.53**	0.22*	−0.56**
2	−0.39**	0.18	0.01	−0.39**	0.16	−0.41**
3	0.43**	0.19	0.29*	0.39**	−0.09	0.45**
4	0.59**	−0.23*	0.56**	0.44**	0.54**	0.32**
5	0.07	−0.39	−0.05	0.15	−0.12	0.24*
All species	0.44**	0.18	0.41**	0.28	0.15	0.32**

[a] * $P < 0.05$, ** $P < 0.01$.

[b] Groups as defined in Fig. 2.

density of vegetation <1 m high ($r = 0.93$, $n = 7$) and the index of insect abundance ($r = 0.92$, $n = 7$) were able to account for the between-season change in bird density.

DISCUSSION

Habitat distribution of migrants: proximate cues.—The significant seasonal shifts in habitat distribution of most migratory species are of interest because of the lack of visible change in many cues that have been suggested or implied to be important settling cues by authors of habitat-selection studies that were conducted during the breeding season (e.g. James 1971, Whitmore 1975).

Although some of the habitat variables predict the density of birds over all habitats and both seasons in this study as well (CANCOV, PSRICH, HEIGHT; Table 3), the same variables do not change seasonally within a habitat (Table 2). Therefore, these habitat variables are unlikely to be the proximate cues used by the birds for a settling response. The other three habitat variables (VEGTOT, VEGONE, ADJINS) did change noticeably from spring to fall, apparently in response to the seasonal summer rainfall that is characteristic of southeastern Arizona (Fig. 4). Some of the birds could have been responding to the surge of vegetative growth near the ground, which was striking in the desert and pine-fir forest habitats and was well correlated with the increase in bird densities in those habitats from spring to fall (Table 4). Holmes et al. (1979) and Beedy (1981) commented that low, understory vegetation represents a unique foraging environment that, when present, is capable of attracting a distinct foraging guild.

Alternatively, the birds could have been responding to changes in food resources independent of vegetation changes, which is possible because VEGONE and ADJINS are not correlated ($r = 0.37$, NS), or to some combination of both variables. Balda et al. (1975) argued that shifts in food availability among habitats best accounted for seasonal shifts in habitat occupancy of transient Flammulated Owls (*Otus flammeolus*), although whether the authors meant to imply a direct response to food availability is uncertain. Austin (1970) also suspect-

TABLE 4. Pearson product-moment correlation coefficients between the magnitude of spring-to-fall change (factor by which spring value is multiplied to give fall value) in bird density and the magnitude of spring-to-fall change in each of the 6 environmental variables.[a] There is a single spring-to-fall calculation for each variable in each habitat ($n = 7$).

Group[b]	VEGTOT	VEGONE	ADJINS	CANCOV	PSRICH	HEIGHT
1	0.42	0.90**	0.87**	−0.24	0.65	−0.52
2	0.89**	0.24	0.29	−0.41	−0.70*	0.22
3	−0.35	0.26	0.27	−0.18	−0.24	−0.01
4	−0.23	0.03	0.02	0.14	−0.06	0.21
5	0.34	0.72*	0.73*	−0.49	0.38	0.09
All species	0.32	0.93**	0.92**	−0.45	0.47	−0.48

[a] * $P < 0.05$, ** $P < 0.01$.

[b] Groups as defined in Fig. 2.

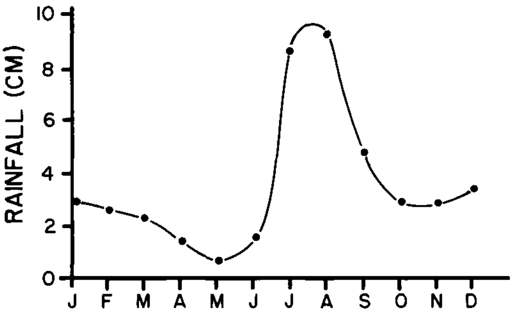

Fig. 4. The yearly pattern of rainfall for southeastern Arizona, as illustrated by 33 yr of data from Portal, Arizona (Green and Sellers 1964).

ed that changes in food availability could account for seasonal shifts in habitat use by the warblers of southern Nevada, but he added that the temperature extremes in the lowlands during fall, rather than a decrease in food availability *per se*, could act to prevent use of such areas by physiologically intolerant species.

Habitat distribution of migrants: ultimate factors.—According to a recent school of thought, as long as it does not limit bird populations, food will be "loosely" exploited and will not be an important factor determining bird species presence and abundance. This idea has led to the development of the "checkerboard" model (Rotenberry and Wiens 1980a, Wiens 1981), in which an unfilled checkerboard represents an unsaturated breeding habitat and a subsection of the board represents one's study plot. From year to year (or place to place within a year) variations in the kinds and abundances of species is very much a stochastic process, determined with about as much certainty by the composition and abundance of checkers within a subset of the checkerboard after the board has been given a vigorous shake. Thus, according to this model, one would not expect a close correspondence between bird population densities and current food resource levels—they would be independent (Fig. 5B). One would expect a close correspondence between bird and food abundance only during an ecological "crunch" (Weins 1977) year, when food resource levels are unusually low relative to bird density (Fig. 5A). At the other extreme is the possibility that, even though food may not be limiting, competition still may exert a significant influence on bird community structure.

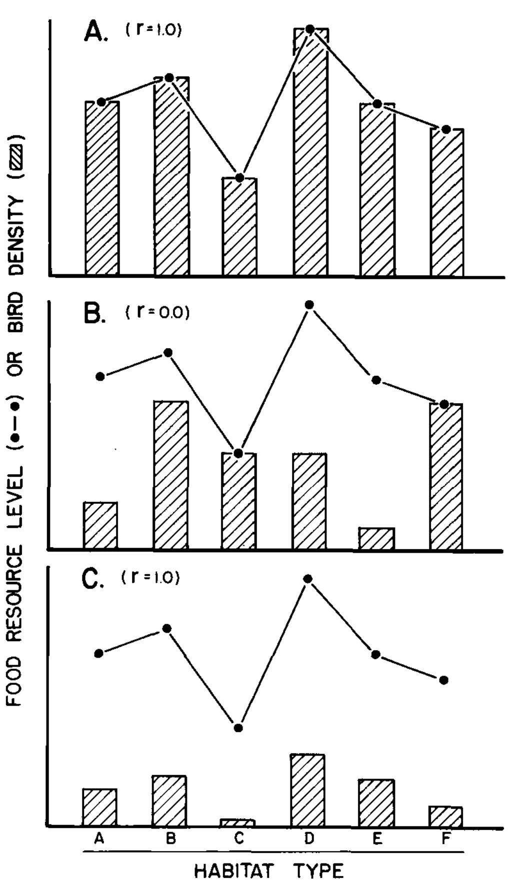

Fig. 5. Graphical representation of the possible relationships between the abundance of a predator (histograms) and its prey (connected dots) across a series of habitat types. (A) The numbers of predators may be limited by prey availability in each habitat, in which case there would be a close correspondence between predator and prey densities. (B) Food may not limit predator populations in most habitats, in which case competition for food will not occur and there will be a poor correspondence between predator and prey densities. (C) Food may not limit predator populations in most habitats, but competition through the economics of foraging will produce a close correspondence between predator and prey densities.

This idea follows directly from optimal foraging theory (Krebs et al. 1983), which assumes that competition is not an all-or-none phenomenon and that, although the strength of competition for food will vary with the degree to which it is limited, food is always limited to some extent and the economics of foraging will demand that birds distribute themselves nonrandomly in space. This results in a close match between food resource production and bird abundance, no matter what the absolute level of food availability (Fig. 5C).

The majority of bird species that passed through southeastern Arizona during migration was distributed significantly differently over the available habitat types in both spring and fall. One can, however, identify groups of these insectivorous species whose seasonal patterns of density and distribution are similar to one another but very dissimilar to members of other such groups. Despite these differences among groups, when considered together, the combined densities of the small, insectivorous bird species match insect densities across habitats within a season (Table 3) and across seasons within a habitat (Table 4) remarkably well. In other words, there are groups of species that respond more or less independently of one another, but when taken together provide a good fit to food resource production. Such a correlation would not be expected according to null models that assume independence between food availability and bird density. The distinction between the predictions that necessarily follow from competition-based, and alternative, null hypotheses cannot be overemphasized. If food resource-based competition is absent, then one would not expect a correlation between food resource availability and numbers of consumers over a variety of sites; instead, all birds would be expected either to go to the same site (i.e. where food is most readily available) because use of food by one individual would not decrease its availability to another, or to distribute themselves randomly with respect to food availability (null model). It is important to appreciate that a null model does not predict, for example, 10 times more birds in a site that has 10 times more food than another site; that would be the case only if the area were 10 times larger.

Alternative hypotheses that do generate predictions consistent with my results include the following: (1) A non-competition-based hypothesis that the populations of both predator (birds) and prey (arthropods) were affected similarly, but independently, by the same mortality factors (e.g. weather). This is most unlikely because the migratory birds are present for a matter of days, and the physical conditions that affect arthropod populations in Arizona undoubtedly are not the same conditions that affect the migratory birds while they are farther north in summer or south in winter. (2) A non-competition-based hypothesis that birds settle in the best habitat (in terms of food availability) until some non-food-related resource (e.g. space) becomes scarce and forces new arrivals to settle in the next best habitat (based on food availability) until it too becomes marginal (in terms of some non-food resource), and so on. On the basis of food availability, the suitability of each habitat (site) would be identical for all birds in this case, but we would not expect a correlation between food levels and bird densities because the relative levels of the non-food-related resources (such as space) would not be expected to be exactly the same as the relative food levels among sites. (3) The non-competition-based hypothesis that each bird species is responding to the presence of a specific prey type. The significant correlation between food availability and bird abundance shown here may exist only because the diversity of prey is itself correlated with my measure of food availability. At this point I have no way to test whether a correlation exists between prey species diversity and my measure of food abundance, but I can test another prediction that necessarily follows from this hypothesis, i.e. that bird species richness is correlated with my measure of food availability. This prediction follows because a diversity of kinds of food would, according to this hypothesis, allow a diversity of bird species to occur in the habitat. Indeed, the correlation is significant ($n = 14$, $r = 0.61$, $P < 0.05$), and such an explanation seems plausible on this basis. It remains for future research to determine whether high seasonal turnover in insect species underlies the high seasonal turnover in bird species within a site, as would also be predicted by this hypothesis. (4) The competition-based hypothesis that "crunch" conditions existed during each year and season that I was present in Arizona. This is unlikely, however, because each of the years was normal in terms of rainfall (Cody 1981: Table 1). Finally, (5) the competition-based hypothesis that food availability determines, in an ultimate sense, the distribution and abundance of the insectivorous bird species during migratory passage. Because the combination of all bird groups provided the best fit to resource availability, this hypothesis would necessitate the presence of interspecific, as well as intraspecific, competition to explain the organization of bird communities at these times of the year.

By what mechanism would birds be able to achieve close matches to food resource levels through competitive adjustments, as would be necessitated by the fifth hypothesis above? According to the "crunch" hypothesis (Wiens 1977), under most environmental conditions it would be rare, if not impossible, for the kinds and densities of species to be able to match resource availability at any particular point in time because the individuals present at that point in time are the survivors or descendants of survivors that were able to "squeeze" through very different environmental conditions at some time in the past (Wiens 1977, Emlen 1981, Emlen and DeJong 1981). However, this view assumes that food levels vary unpredictably and that "... low-fecundity taxa such as many birds and mammals may be quite limited in their capacity to generate population growth sufficient to track variation in food resource levels at all closely" (Wiens 1977: 593). Whether or not the statistically significant but otherwise weak matches between food levels and bird densities demonstrated herein are closer than expected on the basis of the crunch hypothesis is not really clear. Nonetheless, the hypothesis plays down the importance of flexibility in foraging behavior (Alatalo 1980, Hutto 1981), which might enable birds to shift their habitat occupancy or densities within habitats to match current relative food-resource conditions, such as some woodpecker species seem to do within a year following a fire (Blackford 1955, Bock and Lynch 1970, Theberge 1976) or ducks may do from year to year (Nudds 1983). Terrill and Ohmart (1984) also describe a facultative migratory movement pattern of the Yellow-rumped Warbler that apparently is related to food availability.

The habitat shifts reported herein that correspond with shifts in food availability may result from birds being able to "test" several locations before settling in any one for their typical 4-6-day (unpubl. banding records) stopover period. Such resource tracking may be somewhat unique in that adjustments that "fine-tune" bird community composition to resource production may be much easier to accomplish during migration than during other times of the year. It also is possible that, although the relative food levels among habitats change dramatically between seasons, such change is highly predictable and the migrants have been "programmed" to shift their habitat use accordingly. In either case, food availability could be of ultimate importance in producing such a close correspondence between the distribution and abundance of birds and their prey.

These results suggest the possibility that season-to-season or year-to-year differences in bird species composition and densities on a given plot (even breeding-season study plots) may be largely the result of nonrandom food assessment processes such as facultative settlement and migration (Serventy 1971, Ward 1971, Fretwell 1972, Sinclair 1978, Pulliam and Parker 1979, Wiens and Rotenberry 1981, Smith 1982) or "flyover" mechanisms (Nudds 1983). By this I do not mean to suggest that food-based competitive interactions are equally intense at all times and places. Rather, because competition is not an all-or-none phenomenon, the level of competitive interactions that does exist (mediated either directly or indirectly through relative food abundances among or within sites) may be responsible for much of the change that occurs in community structure from one place or time to another. More definitive explanations for the observed shifts in habitat use by these migratory birds must await testing of additional predictions that follow from the plausible alternative hypotheses presented above.

ACKNOWLEDGMENTS

Field work during spring and fall is academically awkward and would have been impossible without the financial support provided by the Frank M. Chapman Fund of the American Museum of Natural History and the Research Advisory Council of the University of Montana. To these organizations I am grateful. I also wish to thank Myra Shulman and Mary Harris for their assistance in the field and Kimball Garrett and Martin Cody for access to their unpublished breeding bird census data. The manuscript benefited from discussions with, and reviews by, S. J. Wright and J. R. McAuliffe and from comments provided by O. Järvinen and anonymous reviewers.

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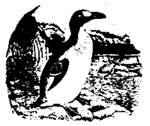
100 Years Ago in The Auk



From "General Notes" (1885 Auk 2: 113–114):

"**Albinism.**—My attention was drawn to a note in the 'Oölogist' for April last, in which the writer gives his experience in albinism and asks for an explanation of these freaks of nature. In order to air my experience, and at the same time to give a probable cause, which I would like, for the sake of possible verification, other observers to look for in the future, is the object of the present note.

"True albinism is of course congenital, and is a condition in which the normal pigmentary matter is deficient in the system of the individual affected; in such cases the eyes are pink, and the skin with its appendages are white or nearly so. In the case of partial albinos, however, it is difficult; their condition can probably be explained by some circumstances occurring after birth which will account for the change in the color of the skin, such for instance as the case given by the writer in the 'Oölogist,' in which the skin had been injured on the back of a Swift, and next year the patch of white feathers indicated the situation of the injury. The same thing is familiar in the case of the horse whose back or shoulder is galled by the harness; white patches appear, owing to lowered vitality of the injured part. These cases are familiar, but I wish to give possibly another cause acting in the same way, only more general. It is this. When a boy I shot among others a black squirrel peculiarly marked, it having a perfectly white tail, with some white about the head; on making a post mortem I discovered through a rent in the intestines a tape-worm about 20 feet in length. Did not wonder then that his head was gray. A few years after a partially white Red-winged Blackbird (*Agelaeus phoeniceus*) was taken, which also contained two or three taenia; next a partial albino Mallard; then a Robin (*Turdus migratorius*) with a white head and mottled back and breast. All were mounted, and are now in my collection. Each of these had two or more tapeworms in their intestines. I am aware that birds, especially some species, are particularly obnoxious to tape-worms, and the above may have been merely coincidences; still it has been observed sufficiently often to make the fact suspicious as a cause of albinism.—G. A. M'CALLUM, *Dunnville, Ont.*"

NUTRIENT RESERVES AND THE ENERGETICS OF REPRODUCTION IN AMERICAN COOTS

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ABSTRACT.—To investigate the bioenergetics of reproduction in American Coots (*Fulica americana*) we collected 108 males and 93 females at Delta Marsh, in southern Manitoba, in 1981. Prenesting and nesting birds were analyzed for fat, protein, and ash content in the nonreproductive tissue. For females, these values were compared to the nutrient requirements of the reproductive tissue during egg-laying. We suggest that feeding conditions before arrival can affect subsequent reproductive output. Fat reserves may function as a threshold that influences the initiation of breeding; protein reserves and time of arrival influence the timing of a nesting attempt. We infer that territory quality is important and that it can result in the termination of laying before nutrient reserves are depleted. By distributing costs of clutch formation before (through nutrient storage) and after (through increased biparental care of eggs and young) clutch formation, the required energy intake concurrent with egg-laying is substantially reduced in female coots. *Received 23 January 1984, accepted 18 August 1984.*

TO understand avian breeding strategies, it is necessary to know the temporal distribution of costs and how nutrients are obtained to meet them (Drobney 1980). Because of the disparity in gamete size, female birds have much greater nutrient demands during reproduction than do males. The male, however, can influence how a female's demands are met (e.g. through nest building and territorial defense), thereby allowing her to spend more time feeding. Recent research has suggested that there is a great interspecific variation in how females and males obtain nutrients for reproduction: most arctic-nesting geese rely almost exclusively on endogenous reserves (Ankney and MacInnes 1978, Raveling 1979, but see Ankney 1984), prairie-nesting ducks (Krapu 1981), Wood Ducks (*Aix sponsa*, Drobney 1980), and Red-billed Queleas (*Quelea quelea*, Jones and Ward 1976) utilize both endogenous and exogenous nutrients, and Brown-headed Cowbirds (*Molothrus ater*, Ankney and Scott 1980) rely on exogenous nutrients. As pointed out by Drent and Daan (1980), however, much more research is needed to evaluate the relative importance of endogenous and exogenous nutrients in affecting clutch size and the timing of breeding in birds.

American Coots (*Fulica americana*, hereafter called coots) are ideal for such research because they show great variation in clutch size (4–17 eggs, Fredrickson 1977) and timing of nesting (Kiel 1954). Also, both sexes incubate (Sooter 1941), and the age of a nesting coot can readily be determined (Crawford 1978). Thus, we undertook to 1) document the timing of acquisition of reserves, 2) describe the energetic cost associated with the formation of a clutch of eggs by coots, 3) determine how much female coots rely on endogenous nutrients for clutch formation, 4) provide an unequivocal approach to assessing the importance of nutrient reserves for clutch formation, 5) describe the dynamics of male body composition during the nesting season, 6) investigate the effects of age on levels of endogenous nutrients, and 7) integrate these results with knowledge about the breeding biology of coots.

METHODS

We collected 108 male and 93 female coots on the Delta Marsh, Manitoba (50°11′N, 98°19′W) from 17 April to 9 July 1981. Coots were assigned to various categories of the reproductive cycle:

Arriving (17 April to 11 May).—Collected from flocks of three or more birds before the first known date of nest initiation.

Paired (29 April to 9 June).—Birds that were with one member of the opposite sex.

Laying (11 May to 9 June).—Males shot flushing from a nest that contained an egg deposited less than 24 h previously, or those that had an incomplete brood patch. Females were separated into subcategories after inspection of their ovaries: *Prelaying* [females with vascularized and yolky follicles (>5 mm), but with no postovulatory follicles (POF)]; *Laying* (ovary with developing follicles and at least one POF); and *Postlaying* (females with no developing follicles but with at least one POF).

Hatching (4-12 June).—Coots that were trapped on the nest at the end of incubation. Most such nests contained pipped eggs or hatchlings.

We used tarsal color, as described by Gullion (1952) and refined by Crawford (1978), to assign coots to one of three age classes (1-, 2-, or >2-yr-olds).

Carcass analysis.—Birds were weighed, plucked, and reweighed to the nearest 1.0 g on the day of collection. The ovary and oviduct were removed from females and the testes from males. Carcasses (minus the reproductive organs) were double-bagged, labeled, and frozen.

Carcasses were later thawed and the liver, gizzard, and intestines, with caeca attached, were removed. These organs were cleaned of adhering fat and weighed to the nearest 0.1 g. The weight of the digestive tract contents was determined as the difference in weight between the cleaned and uncleaned organs making up the tract. Body weight reported here is the fresh weight of a coot minus the weight of the contents of its digestive tract.

Breast and leg muscles, as defined by Ankney and MacInnes (1978), were excised (left side only) and weighed. All organs described and the rest of the carcass including head, wings, and feet were dried to constant weight (0.1 g) at 80-100°C (see Kerr et al. 1982). The dried leg and breast muscles were each passed twice through a Wiley mill. The remaining dried organs and carcass were ground together at least 3 times using a hand-operated meat grinder. The leg and breast muscles and about 15 g of the dried carcass were analyzed separately for lipid content by extraction with petroleum ether in a Soxhlet apparatus. Values for lean dry weight (LDW) of breast and leg muscle were doubled and are presented herein.

Dry body weight was the sum of the weights of all dried components excluding the ovary, oviduct, and feathers. Fat reserve was the sum of breast fat, leg fat, and carcass fat and refers to the fat present in adipose cells of the nonreproductive tissue. Fat reserve was subtracted from dry body weight to yield the LDW of the nonreproductive tissue. Our definition of "nutrient reserve" is the measure of a fraction (fat, protein, or mineral) of the whole bird (excluding feathers, ovary, oviduct, and testes) that may respond to nutritional demands of egg synthesis or other changes in energy balance. Conversely, we refer to the eggs, follicles, oviduct, and testes as reproductive tissue.

LDW can be used to index protein, but this relationship may be confounded by variation in ash (i.e. mineral, Ricklefs 1974: 161) content. The skeleton is the major source of ash (Robbins 1983: 211). In female birds variation in ash may result from the daily cycling of medullary bone, or a continual decline in cortical bone that can function as a mineral reserve for eggshell synthesis (Taylor and Moore 1954). Medullary bone is not present in males (Simkiss 1975: 307) so changes in LDW must parallel changes in protein. Thus, the following procedure was applied only to females. A sample of about 15 g from each dried, ground carcass was placed in a muffle furnace for 6 h at 550°C. The residue was used to calculate the ash content for each bird that, when subtracted from body LDW, yielded the ash-free LDW, an index of protein.

TABLE 1. Ages and numbers of female and male coots from arriving (ARR) and paired (PRD) samples.

	Age	ARR	PRD
Females[a]	1	7	12
	2	7	9
	>2	13	3
Males[b]	1	13	8
	2	16	8
	>2	12	9

[a] $\chi^2 = 7.67$; $P < 0.025$.
[b] $\chi^2 = 0.43$; $P < 0.50$.

Reproductive organ analysis.—Both testes were weighed to the nearest 0.01 g and discarded. The ovaries and oviducts were weighed and, except for those removed from prelaying and laying females, discarded. Large yolky ovarian follicles were removed from ovaries of prelaying and laying females, weighed, placed in a drying oven with the weighed oviduct, and dried to constant weight at 90°C. Lipids were extracted from developing follicles with petroleum ether in a Goldfisch apparatus. Dry follicle weight minus lipid weight yielded the LDW of each follicle. Carbohydrates and minerals comprise only 2% of chicken egg yolks (Romanoff and Romanoff 1949), so we hereafter refer to the LDW of developing follicles and egg yolks as yolk protein.

From 17 nests we removed fresh eggs, weighed them, and heated them in a 70°C water bath to ease separation of yolk from albumen (after Lack 1968). Eggshell membranes were peeled away from shells and added to the egg white. These membranes consist mainly of protein with a minute amount of carbohydrate (Sturkie 1976: 318); because deposition of both egg white and membrane around the yolk is complete in 4-6 h (Sturkie 1976: 318), we refer to them collectively as albumen. The shell, yolk, and albumen were weighed separately and dried to constant weight at 80-90°C. Eggshell thickness was the mean of 5 measurements (to the nearest 0.02 mm) made with calipers on each egg. Ether-extractable lipids were removed from dried yolks in a Goldfisch apparatus. In this way, yolk lipid, yolk protein, albumen, shell weight, and shell thickness were determined for 98 coot eggs.

The exclusion of badly damaged organs or egg

TABLE 2. Changes in body composition and dried organ weights (g) of male coots during the nesting season. ARR = arriving, PRD = paired, LAY = laying, HTC = hatch. Values are $\bar{x} \pm 1$ SE, with sample sizes in parentheses.

		Prenesting		Egg-laying		Incubation	
Variable	ARR	P[a]	PRD	P	LAY	P	HTC
Body weight	575.2 ± 10.2 (41)	NS	595.9 ± 11.3 (25)	NS	611.6 ± 7.6 (24)	NS	584.3 ± 13.7 (11)
Fat	39.5 ± 4.8 (40)	NS	32.4 ± 4.1 (22)	NS	32.5 ± 3.3 (22)	NS	27.1 ± 3.8 (11)
Protein	126.9 ± 1.9 (40)	NS	130.5 ± 3.0 (22)	*	139.4 ± 2.1 (22)	NS	141.4 ± 3.7 (11)
Breast LDW	16.4 ± 0.4 (41)	NS	16.7 ± 0.6 (22)	NS	16.2 ± 0.4 (22)	NS	15.6 ± 0.5 (11)
Leg LDW	18.8 ± 0.4 (41)	**	21.8 ± 0.8 (24)	**	24.4 ± 0.4 (24)	NS	24.5 ± 1.0 (11)
Liver	4.07 ± 0.12 (41)	NS	4.02 ± 0.20 (25)	NS	4.20 ± 0.11 (24)	**	5.08 ± 0.27 (11)
Gizzard	10.46 ± 0.31 (41)	NS	9.66 ± 0.39 (25)	NS	9.66 ± 0.35 (24)	NS	9.30 ± 0.46 (11)
Intestine	4.56 ± 0.23 (40)	NS	4.79 ± 0.34 (25)	NS	5.08 ± 0.39 (24)	NS	5.77 ± 0.31 (11)

[a] P = significance level of t-test between means in adjacent columns. * $P < 0.05$; ** $P < 0.01$; NS indicates $P > 0.05$.

components from analyses led to variation in sample sizes.

Results

Arrival Chronology

Age and sex of individual coots were determined after collection; we assumed that our samples were unbiased and represented the proportion of different-aged coots present in the population of arriving and paired birds (see Methods).

Female age ratios were not independent of prenesting status (Table 1); 48% of the arriving, but only 12.5% of the paired female sample were >2-yr-olds. This indicates that when arriving coots were collected, a large proportion of the younger females had not yet reached the breeding grounds. Male age ratios did not change from arrival to pairing (Table 1).

Male Body Composition

Male coots arrived on Delta Marsh with high levels of fat. No segment of the nesting season caused a change in male fat reserves (Table 2), but their fat reserves were lower at the end of incubation than at arrival (t = 2.02, df = 49, $P < 0.05$).

Endogenous protein in males increased during the laying period (Table 2). Thus, unlike fat, protein was accumulated on the breeding grounds.

Male leg muscle increased in weight during prenesting and egg-laying (Table 2). During incubation, liver weight increased to a maximum, temporally corresponding to maximum protein levels. No changes were detected in any of the other organs.

There was no consistent relationship between fat reserves and age in male coots (two-way ANOVA, $P > 0.50$). However, oldest males consistently had the highest protein levels in all reproductive categories (Fig. 1), partly because they were structurally largest (Alisauskas unpubl. data). Male protein was correlated with testes weight ($r = 0.465$, df = 100, $P < 0.001$).

Nutrient Reserves of Prenesting Females

Female arrivals had relatively larger fat reserves (accounting for 26.6% of dry body weight) than males (21.8%; t-test on arcsine transformed percentages, t = 2.45, df = 64, $P < 0.02$). Absolute fat and mineral reserves of females did not change during prenesting (Table 3).

Protein was accumulated after arrival, with hypertrophy of leg muscle accounting for 31.5%

of the increase (Table 3). Liver weight increased significantly, but weights of the other digestive organs and of flight muscles did not change. Increases in ovary weight of prenesting females were positively correlated with endogenous protein ($r = 0.428$, df = 43, $P < 0.01$), but not with fat reserves ($r = 0.107$, df = 46, $P > 0.05$) or minerals ($r = 0.172$, df = 43, $P > 0.05$).

Fat and protein reserves were not related to the age of prenesting female coots (two-way ANOVA, $P > 0.5$ and $P = 0.3$, respectively). Ovarian recrudescence was most advanced in the oldest females at arrival, but age-related differences were not significant among paired birds (Table 4), possibly because the sample size of older birds was small.

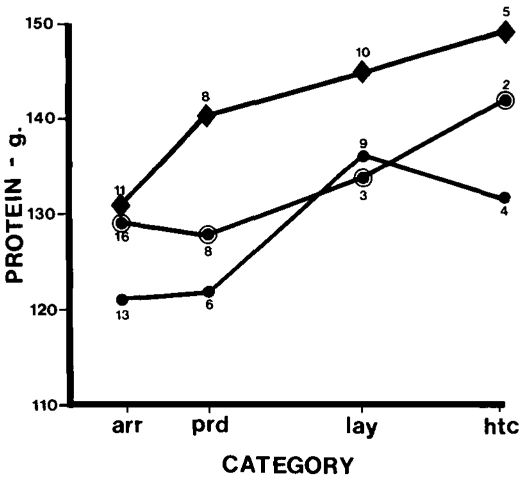

Fig. 1. Mean protein reserves (g) of breeding male coots in relation to age. Numbers beside points indicate sample sizes; closed circles are 1-yr-olds, double circles are 2-yr-olds, and diamonds are >2-yr-olds.

IMPORTANCE OF NUTRIENT RESERVES FOR CLUTCH FORMATION

We investigated the relative importance of endogenous vs. exogenous nutrients in egg production. First, we determined the fat, protein, and mineral fractions of the reproductive tissue (ovary, oviduct, and eggs) for female coots in various stages of rapid follicular development (prelaying, laying) and regression (immediate postlaying). We then compared the nutrients present in the reproductive tissue of individual females with their nutrient reserves (i.e. in their somatic tissue).

We defined "reproductive fat" as the sum of fat present in the ovary and total fat present in eggs already laid (as evidenced by the number of postovulatory follicles). "Reproductive protein" was the sum of the protein present in the ovary, the oviduct, and the total albumen and yolk protein of eggs laid (including oviducal eggs).

Significant variation in yolk lipids, yolk proteins, and albumen were a result of, and inversely related to, laying sequence ($r^2 = 39.8\%$, $P < 0.001$; $r^2 = 11.5\%$, $P < 0.001$; and $r^2 = 8.8\%$, $P < 0.01$, respectively). Dry eggshell weights declined with laying sequence ($r^2 = 7.8\%$, $P < 0.01$), but laying sequence had no effect on shell thickness ($r^2 = 2.8\%$, $P > 0.05$). We used the mean value of each component, relative to egg sequence (Fig. 2), to estimate nutrient commitments to eggs.

Effect of clutch formation on nutrient reserves.—We used one-tailed tests of significance for regression analysis of nutrient reserves (Y) on nutrients committed to reproduction (X) because, a priori, if female coots used nutrient reserves to form eggs, then clutch formation would cause a decline in those reserves (i.e. we expected the slope to be negative). Regression analysis is useful because the slope provides an estimate, with measures of variance, of the proportion of the clutch formed with endogenous nutrients. The 95% confidence interval of the intercept gives a measure of the minimum amount of reserve that an individual bird possesses before egg formation starts.

Figure 3 illustrates changes in reserves with respect to nutrients committed to the reproductive organs. Seven prelaying, 8 laying, and 6 postlaying females that had completed laying within a day or two were used in the analyses. The status of 2 of the prelaying females was questionable, as we suspect that they would not have initiated a laying cycle. Although they were classified according to our a priori definition of a prelayer (see Methods), their nutrient commitment to follicular growth was relatively slight, and there was no guarantee that they would have laid. We provide the results of the analyses both with and without these 2 individuals in the sample (Fig. 3, Table 5). In all cases except one, the results were significant ($P < 0.05$), whether or not these females were included. However, we think that the analyses

TABLE 3. Changes in body composition and dried organ weights (g) of prenesting female coots. ARR = arriving, PRD = paired. Values are $\bar{x}$ ± 1 SE, with sample sizes in parentheses.

Variable	ARR	P^a	PRD
Body weight	459.7 ± 9.1 (24)	*	498.0 ± 11.9 (24)
Fat	39.2 ± 5.1 (26)	NS	33.5 ± 5.1 (24)
Ash	14.9 ± 0.4 (25)	NS	15.8 ± 0.6 (21)
Protein	83.1 ± 1.9 (25)	**	90.2 ± 1.6 (21)
Breast LDW	13.6 ± 0.5 (26)	NS	14.1 ± 0.4 (24)
Leg LDW	14.6 ± 0.4 (27)	***	16.9 ± 0.4 (24)
Liver	3.37 ± 0.12 (27)	**	4.19 ± 0.22 (24)
Gizzard	8.19 ± 0.27 (27)	NS	8.37 ± 0.38 (24)
Intestine	3.90 ± 0.22 (27)	NS	4.20 ± 0.19 (24)

[a] P = significance level of t-test between means in adjacent columns. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS indicates $P > 0.05$.

that excluded these birds provided a better representation of nutrient-reserve use by female coots.

Female coots used endogenous fat and protein for clutch formation (Fig. 3, Table 5). For every gram of reproductive fat produced, fat reserves, on average, declined 0.85 g. The lower confidence limit of the intercept (or the average amount of fat reserve before any allocation to rapid ovarian growth) was 27.5 g; thus, we conclude that this value corresponds to a threshold above which 97.5% of females would initiate a laying cycle. Endogenous protein was less important as a reserve, providing only 28% of the egg protein requirements. Ash content did not vary as a result of eggshell synthesis.

Of the organs investigated that made up the endogenous protein fraction, only breast and leg muscle showed a consistent negative relationship with reproductive protein commitment (Table 5); the decline in LDW of these organs accounted for half the decline in total body protein. Regression analysis showed that variation in gizzard weight was unaffected by reproductive protein allocations. The results for intestinal weight were equivocal.

It is noteworthy that some birds had completed laying even though they possessed more fat and protein reserves than birds that were still laying when collected (Fig. 3).

Energy budget of egg-laying females.—To construct an energy budget, several physiological variables must be measured: the daily laying rate, the follicular growth rate, the number of days required to complete rapid follicular growth, the oviducal growth rate, the amounts of fat and protein in the ovary, and the albumen content of an egg.

Removal of eggs from nests during this study substantiated Sooter's (1941) assertion that coots lay 1 egg/day. With this laying rate, the difference in weight between any two consecutively developing ovarian follicles is the growth of the larger follicle over 24 h (Ricklefs 1974). We thereby quantified daily nutrient allocation associated with producing the yolk fat and protein.

Coots that had at least one POF never had >7 developing follicles. Thus, it takes 7 days for a follicle in the rapid-growth stage to attain maturity, i.e. from the first noticeable increase in ovum size (day −8) until ovulation (day −1). The predicted length of the rapid-growth phase, as a function of egg mass, was 7.3 days [Walsberg's (1983: 175) equation].

Oviduct weights of prelaying females were

TABLE 4. Comparisons (one-way ANOVA) of ovary wet weights (g) of female coots by age within breeding status during prenesting. ARR = arriving, PRD = paired. Values are $\bar{x}$ ± 1 SE, with sample sizes in parentheses.

Breeding status	Age			P^a
	1	2	>2	
ARR	0.559 ± 0.065 (7)	0.624 ± 0.065 (7)	0.835 ± 0.062 (11)	*
PRD	1.057 ± 0.160 (11)	1.184 ± 0.216 (9)	1.450 ± 0.165 (3)	NS

[a] * $P < 0.05$; NS indicates $P > 0.05$.

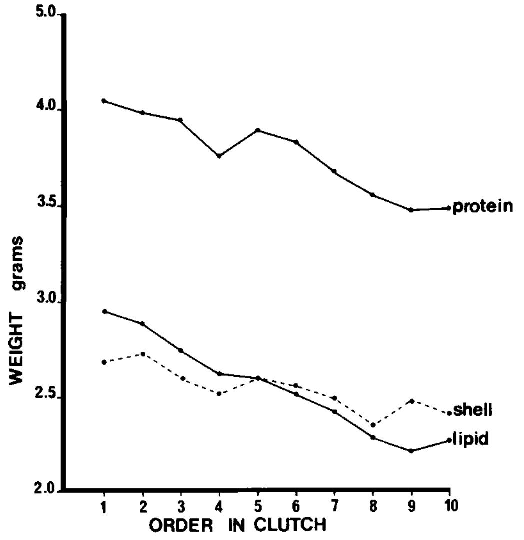

Fig. 2. Decline in mean nutrients (g) in coot eggs with respect to laying sequence.

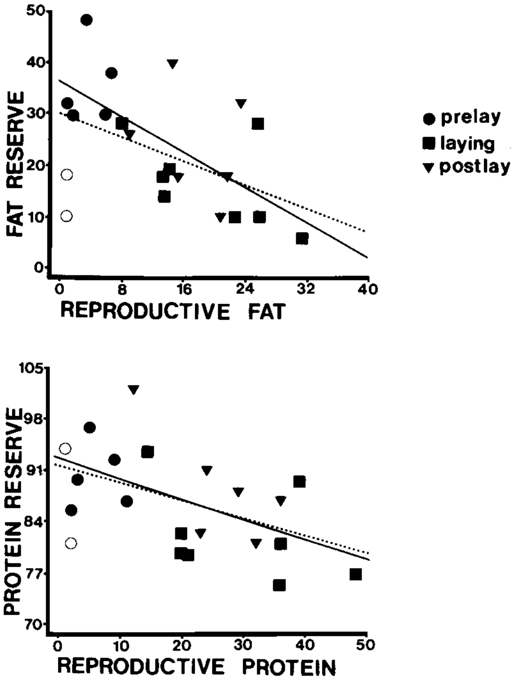

Fig. 3. Decline of fat and protein reserves (g) related to increase in allocation of fat and protein (g), respectively, to "reproductive tissue" in female coots during clutch formation. Open circles represent females 168 and 206 (see text). Dotted and solid lines are fitted using least-squares regression with and without females 168 and 206, respectively.

placed in categories of days-from-ovulation (based on the weight of the heaviest follicle in the hierarchy). The relationship between oviduct dry weight (Y) and day from ovulation (X), based on data for days −8, −7, −5, −3, −1, was described by the equation

$$\log_{10}Y = 0.858 + 0.14X$$
$$(r^2 = 99.6\%, P < 0.05), \qquad (1)$$

which we used to estimate dry oviduct weights for days −6, −4, and −2.

The daily production of each nutrient in the ovary, the oviduct, and the first 8 eggs was used to estimate the cost of producing an 8-egg clutch. To determine the relative importance of reserves in terms of female energy expenditures during clutch formation, 1 g of stored fat was assumed to equal 37.67 kJ (Ricklefs 1974: 160). For protein, an energy equivalent of 23.86 kJ/g was used (Kleiber 1961). Body water and ash were not considered in the energy budget because they have no available chemical energy (Robbins 1983: 213). Because the conversion of unprocessed material to egg nutrients is not 100% efficient, the total cost of producing an egg is greater than the energy content in the egg. Brody (1945) gave 77% as the production efficiency for the synthesis of eggs. However, this value applies to the conversion of dietary nutrients to egg nutrients. Costs of biosynthesis associated with protein accumulation and the conversion of digestible carbohydrates to fat at the time of storage should not be incorporated into costs that a female incurs at the time of egg-laying. Efficiency values for the conversion of nutrient reserves to egg components are not available but are undoubtedly greater than 77%; because we lacked an empirical alternative, we assumed 100% efficiency, but those portions of the egg requirements met exogenously were divided by 0.77 to incorporate the cost of biosynthesis concurrent with clutch formation. To account for the difference in conversion efficiency of stored vs. dietary nutrients, the appropriate correction between the amount of nutrients in the clutch and a female's expenditures in providing them would be:

$$C = E[RP_R^{-1} + (1 - R)P_D^{-1}], \qquad (2)$$

where C = cost to female (kJ) in producing 1 g of egg nutrient, E = energy equivalent of egg

TABLE 5. Summary of regression analysis of Y (nutrient reserves) on X (nutrient commitment to clutch formation). Analyses with $n = 19$ do not include females 168 and 206 (see text and Fig. 3).

Y	X	n	Intercept[a]	Slope[a]	r^2	P[b]
Fat reserve	Reproductive fat	21	30.2 ± 8.4	−0.55 ± 0.52	20.9	**
		19	36.1 ± 8.6	−0.85 ± 0.51	42.5	**
Protein reserve	Reproductive protein	21	91.3 ± 5.0	−0.24 ± 0.20	24.3	*
		19	92.6 ± 5.6	−0.28 ± 0.22	30.2	**
Fat reserve and protein reserve	Reproductive fat and reproductive protein	21	121.4 ± 11.7	−0.36 ± 0.29	26.6	**
		19	128.6 ± 12.7	−0.51 ± 0.30	42.9	**
Ash	Shell	21	16.6 ± 1.1	0.003 ± 0.08	0	NS
		19	16.4 ± 1.3	0.010 ± 0.09	0.3	NS
Breast LDW	Reproductive protein	21	13.5 ± 1.5	−0.07 ± 0.062	23.0	*
		19	13.3 ± 1.8	−0.07 ± 0.07	19.0	*
Leg LDW	Reproductive protein	21	17.9 ± 1.4	−0.06 ± 0.058	19.5	*
		19	18.2 ± 1.7	−0.08 ± 0.065	22.2	*
Gizzard weight	Reproductive protein	21	7.74 ± 1.0	−0.031 ± 0.041	11.9	NS
		19	1.39 ± 1.2	−0.020 ± 0.046	4.6	NS
Intestine weight	Reproductive protein	21	4.47 ± 0.7	−0.020 ± 0.029	9.4	NS
		19	4.84 ± 0.8	−0.031 ± 0.010	21.7	*

[a] ±95% confidence interval.

[b] Probability that $r = 0$: * $P < 0.05$; ** $P < 0.01$, NS indicates $P > 0.05$.

nutrient (kJ/g), R = proportion of egg nutrients supplied by female reserves, $(1 - R)$ = proportion of egg nutrients supplied directly by the diet, P_R = efficiency for converting nutrient reserves to egg nutrients = 1.00, and P_D = efficiency for converting dietary nutrients to egg nutrients = 0.77. For example, for each gram of egg lipid produced, the female would expend $37.67(0.85 + 0.15/0.77) = 39.36$ kJ. For egg-protein synthesis, C is equivalent to 28.99 kJ/g. Equation 2 would apply to any strategy of nutrient reserve use, but values of C for fat and protein would be species-specific.

Daily energy costs of providing each egg nutrient were estimated by multiplying the actual nutrient allocation by the corrected conversion from Eq. 2. We modeled the energy budget for an 8-egg clutch for two reasons. First, although there was a significant inverse relationship between the size of a clutch and its initiation date ($r = -0.679$, df = 60, $P < 0.001$; Fig. 4), the removal of eggs involved 17 clutches that began between 12 and 26 May. The mean clutch size of all nests on the study area begun during that time was 8.3. Second, laying females had, on average, 4.9 developing follicles and 3.3 post-ovulatory follicles, i.e. the mean potential clutch size of birds in this first wave of nesting (see Fig. 4) was 8.2 eggs.

The temporal distribution of energy expenditures by females producing 8 eggs spans 15 days (Fig. 5). Maximum costs would be incurred by females only during days 0 and 1. The average weight of laying females was about 500 g. Basal metabolic rate (BMR) was estimated as 185 kJ/day, using the equation of Aschoff and Pohl (1970) for resting nonpasserines. Thus, maximum cost of egg formation (about 223 kJ/day) corresponds to about 121% of the BMR of laying females. Coots laying clutches smaller than the number of days needed for follicle growth (i.e. 7) would not reach this maximum. These results empirically support King's (1973) model for the temporal distribution of energy expenditure for egg synthesis by birds in general.

The estimated total cost of production over the 15 days was 1,830 kJ. The greatest demands would be for yolk synthesis, with yolk lipids requiring the largest commitment (43.7%) from the energy budget. Albumen would account for 27.1%, yolk proteins 21.9%, and the oviduct 7.3% of a female's total expenses as she produced an 8-egg clutch.

Effect of declining egg weight.—We reestimated costs assuming all eggs were equal in energy content to the first egg. This increased the total estimated requirements for clutch formation by 9.0% (Fig. 5). The greatest increases would be 15.8% for yolk proteins and 12.0% for yolk lip-

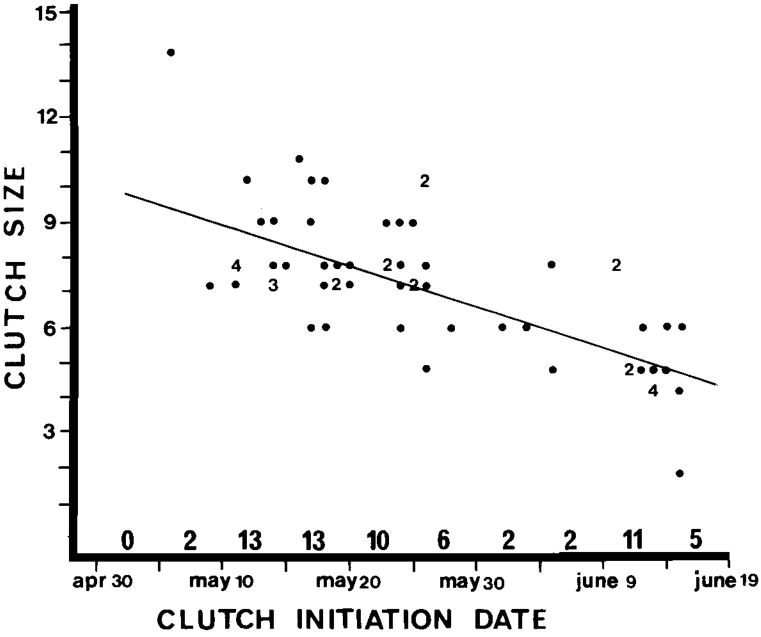

Fig. 4. Relationship between clutch initiation date and clutch size in coots; numbers above the x-axis are nests initiated per 5-day interval.

ids. Albumen allocation varied little from first to last egg and increased the estimated cost by only 1.2%. Costs in producing the oviduct would not change because a minimum size is presumably required to accommodate the first egg, which is the largest, in all cases. Thus, the sequential decline in egg size reduced the estimated expenditures over the 15 days.

Because most egg lipids are supplied endogenously, the amount of egg lipid produced presumably depends on the fat reserves that females possessed immediately before rapid ovarian growth. First eggs of a clutch had an average of 2.95 g of yolk lipid. A clutch of 8 consecutively smaller eggs contained 21.0 g of lipid. Hypothetically, if females allocated the same amount of fat reserves to subsequent eggs as they did to the first egg, there would only be enough stored fat for 7 instead of 8 eggs (21.0 g/2.95 g = 7.1).

NUTRIENT RESERVES OF INCUBATING FEMALES

There was no change in body weight, fat reserves, or protein reserves of incubating females. Of the organs investigated, only intestine weights increased (df = 21, $P < 0.001$).

DISCUSSION

MALE NUTRIENT RESERVES

Oldest males had the highest levels of endogenous protein before and during the nesting season (Fig. 1). Ryan and Dinsmore (1980) found that the oldest male coots were the most aggressive. Ankney (1977a) suggested that large muscles and physical strength of male Snow Geese (*Chen caerulescens*) were important for defending the female during nesting. Thus, for a species such as the coot where nest sites appear to be a limiting factor (see Sugden 1979, Crawford 1980) and must be acquired and maintained by intraspecific aggression, older males should be most successful because of greater physical strength and aggressive behavior. Greater male age also may be partially responsible for the increased reproductive success of older females documented by Crawford (1980), who found that pairing by coots usually involved birds of similar age.

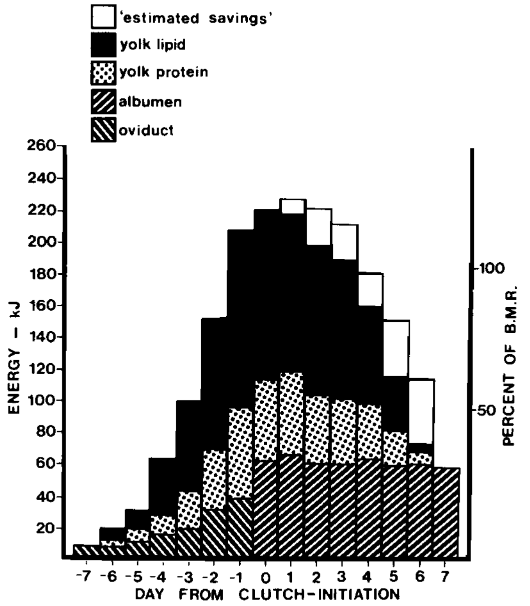

Fig. 5. Cumulative daily expenditures of female coots producing a clutch of 8 eggs expressed in kJ and as a daily percentage of daily basal metabolic rate (BMR). "Estimated savings" are the daily differences in cost for clutches composed of eggs with sequentially declining nutrient contents and a hypothetical case where eggs receive nutrient allocations equal to that of the first egg.

FEMALE NUTRIENT RESERVES

Fat and protein.—The critical level of fat reserves, above which most females would nest, was 27.5 g in 1981. Moreover, most (85%) of the lipids required for egg production came from reserves. This suggests that the size of a female's fat reserves influences whether she will nest (see Drent and Daan 1980) and her clutch size, as demonstrated in Snow Geese (Ankney and MacInnes 1978).

Coots did not store fat after arrival on the breeding grounds. This is similar to what occurs in Mallards (*Anas platyrhynchos*, Krapu 1981) and Snow Geese (Ankney and MacInnes 1978); in these species, weather conditions on the wintering grounds or during spring migration affect subsequent recruitment (Heitmeyer and Fredrickson 1981, Boyd et al. 1982). Thus, feeding conditions on the wintering grounds and/or during spring migration influence the ability of female coots to store fat and consequently to reproduce.

Krapu and Doty (1979) showed that among prenesting female Mallards, adults had consistently larger fat reserves than did yearlings, and the adults laid earlier and had larger first clutches. Although Crawford (1980) reported that older female coots laid larger clutches and typically nested earliest, we found no consistent relationship between fat reserves and age in prenesting females. We suggest that earlier nesting by older females occurs because they arrive earlier than 1- and 2-yr-old females. Clutch-initiation dates were bimodally distributed in 1981 (Fig. 4), which is common in the nesting phenology of coots (see Kiel 1954, Fredrickson 1970, Sugden 1979, Crawford 1980). Territoriality and the distribution of nesting cover are the main factors influencing the dispersion of coot nests (Sugden 1979). The delayed breeding of some individuals is related to the availability of nesting habitat associated with the new growth of emergent vegetation (Sugden 1979, Crawford 1980); younger females are primarily responsible for the second wave of nesting. This suggests that there is an advantage in arriving early, and among females, >2-yr-olds arrived earliest (Table 1).

Ovarian size in prenesting coots was positively correlated with age (Table 4) and with protein reserves. In those species storing nutrients for reproduction, the size of their protein reserves may proximately control the timing of a breeding attempt (see Ashmole 1971, Jones and Ward 1976, Drent and Daan 1980). Ovary weight was correlated with the levels of both fat and protein reserves in Snow Geese during spring migration (Wypkema and Ankney 1979). We suggest that in coots, fat reserves allow the female to "evaluate" whether she possesses the minimum required for a breeding attempt; if this is satisfied, then the rate of acquisition of protein reserves, in addition to time of arrival, influence the timing of breeding. Nesting coots show high levels of inter- and intraspecific aggression against intruders on their territories (Gullion 1953). Given such spacing behavior, pairs with females that have the largest protein reserves at arrival or that acquire protein most rapidly after arrival probably nest earliest.

Minerals.—Coots did not store long-term mineral reserves. Ash content did not change through laying (Table 5), indicating that there was no depletion of cortical bone, i.e. long-term mineral reserve (see Simkiss 1967: 173, Ankney and Scott 1980). Taylor and Moore (1954) showed that weight of cortical bone declined but that of medullary bone remained constant when laying hens were fed a low-calcium diet. Coots presumably met all of their calcium requirements without storing or using minerals in the cortical bone.

On the Delta Marsh, sources of dietary calcium appeared to be abundant (see Alisauskas 1982). Calcium deficiency is known to cause eggshell thinning in laying hens (Taylor and Moore 1954), but in laying coots, although shell weight declined with egg sequence (i.e. as the eggs decreased in size), shell thickness did not. Therefore, the calcium requirements of eggshell formation were not greater than what females could acquire daily from their territories.

Control of clutch size.—While levels of endogenous fat probably control the initiation of rapid ovarian growth, termination may result before fat or protein reserves are depleted. Most of our postlaying females retained levels of fat and protein greater than birds that still had not completed laying (Fig. 3). This suggests that exogenous nutrients, and therefore territory quality, may regulate clutch size. Coots rarely wander far from their territories before hatch (Ward 1953). Thus most protein and all minerals for egg synthesis must be acquired from areas established as territories before nesting. Given that a female has sufficient fat reserves to start a clutch, the number of eggs laid may be correlated with some empirical measure of territory quality (i.e. the availability of materials amenable for conversion to egg proteins and eggshells). Age-related differences in foraging efficiency among individual females, or the physique of their mates (see above), might somewhat confound such a relationship. Clearly, selection and defense of territories are important steps toward acquiring sufficient exogenous proteins and minerals. This may explain the aggressive nature of nesting coots.

Reduction of daily expenditures for egg-laying.—To determine the increase in daily energy intake necessary to meet the added costs of egg production, it is appropriate to relate reproductive costs to the daily energy expenditure (DEE) of nonbreeding females. A nonbreeding 500-g coot (the weight of the average laying female) would require 568 kJ of energy/day (from Walsberg 1983: 193). Given a conversion efficiency of 77%, this bird would have to ingest 738 kJ/day to balance DEE. On day 0 of clutch formation (see Fig. 5), when energy demands for eggs are maximal, females must provide 3.88 g of protein, of which 72% (2.79 g) must be exogenous. To do this, at a conversion efficiency of 77%, the female must consume 3.62 g (86.6 kJ) on the same day. At the same conversion efficiency, she also must consume 22 kJ of material to provide 0.43 g of egg lipid. Therefore, to meet the costs of egg production, laying females would have to increase their daily energy intake by 109 kJ per 738 kJ, or by 14.8% above what is required for DEE. If females relied entirely on exogenous nutrients for clutch formation, the required intake on day 0 would be 261 kJ, or 35.4% more energy relative to the DEE of a nonbreeding female. Therefore, storage of reserves before nesting reduced the energy intake required on day 0 of clutch formation from 35% to 15% above that needed concurrently for DEE. We emphasize that our calculations provide only rough estimates of the energy cost of egg formation because precise estimates of conversion efficiencies are unavailable. Clearly, there is a need for research to determine the specific production efficiencies of converting endogenous and exogenous fat and proteins (and carbohydrates) into egg nutrients.

Decreases in egg size with laying sequence also reduced energy requirements (Fig. 5) during the second half of the laying cycle. Egg lipids showed the most consistent decline. Reduced lipid allocation began immediately after the first egg, before reserves declined to basal levels, and allowed an extra egg to be produced. Thus, if all young survive, such as when food is abundant, parental fitness would be increased by $^8/_7$, or 1.14 times. From this result, we suggest that studies on energy budgets in birds should question the assumption of constant egg weight relative to laying sequence, as this may affect estimates of energy expenditure for an entire clutch.

Incubation.—Maximum weights of the liver of males, and of the gizzard and intestine of females at this time, strongly suggest that feeding is important to coots during incubation. Intestine weight and length in birds are known to be sensitive to changes in diet quality (Pendergast and Boag 1973, Miller 1976). The diet of coots at this time is most likely vegetation with high levels of fiber, leading to the increased mass of digestive organs that we observed. Anorexia resulting in weight loss during incubation was suggested for Lesser Snow Geese (Ankney 1977b), and demonstrated in

Red Junglefowl (*Gallus gallus spadicus*, Sherry et al. 1980) to functionally alter energy balance. Coots remain active during incubation (Ryan and Dinsmore 1979), and continued feeding resulted in high levels of protein at hatch in 1981. Because both sexes incubate, female coots are released from having to rely on body reserves as an energy source during incubation. Moreover, this allows females to use most of their fat reserves for egg formation. Thus, incubation does not affect body weight of female coots as it does in many waterfowl species (see Gatti 1983). An exception to this may be found in the hole-nesting Wood Duck, which can incubate a clutch without significant weight loss and without male assistance (Drobney 1980).

ACKNOWLEDGMENTS

We thank M. Anderson, B. Batt, K. Bedford, J. Black, P. Kehoe, D. MacLaughlin, M. Madore, H. Murkin, J. Nelson, and A. Young for their field assistance. R. Crawford, W. Eddleman, and D. Scott offered valuable advice during the study. P. Handford, D. Krementz, J. Millar, and D. Scott reviewed earlier drafts of the manuscript; P. Jones, R. Drobney, and an anonymous reviewer contributed to a later draft. This work was funded through grants from the Delta Waterfowl Research Station of the North American Wildlife Foundation and through the Natural Sciences and Engineering Research Council of Canada support to Ankney.

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The **XIX International Ornithological Congress** will be held in Ottawa, Canada, from **22 to 29 June 1986.** Prof. Dr. Klaus Immelmann is President. The scientific program will include plenary lectures, symposia, contributed papers (oral and posters), round-table discussions, special-interest group meetings, and workshops. Pre- and post-congress excursions and workshops are planned, as well as early morning bird walks and other activities for members and accompanying members. The deadline for registration and submission of contributed papers is **January 1986.** Additional information, the final circular, and registration forms are available from: **Dr. Henri Ouellet, Secretary General, XIX Congressus Internationalis Ornithologicus, National Museum of Natural Sciences, Ottawa, Ontario K1A 0M8, Canada.**

by incubating White-winged Doves. Pp. 107–112 *in* Physiological systems in semiarid environments (C. C. Hoff and M. L. Riedesel, Eds.). Albuquerque, Univ. New Mexico Press.

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The **1985 Raptor Research Foundation International Meeting and Symposium on the Management of Birds of Prey** will be held at the Capitol Plaza Holiday Inn in Sacramento, California, **2-20 November 1985**. For more information or if you are interested in presenting a paper, contact **Dr. Richard R. Olendorff, U.S. Bureau of Land Management, 2800 Cottage Way, Sacramento, California 95825,** or **Nancy Venizelos, San Francisco Zoological Society, Sloat Boulevard at the Pacific Ocean, San Francisco, California 94132.**

The third edition of the **International Code of Zoological Nomenclature** can be ordered through the **American Association for Zoological Nomenclature, Room W-115, National Museum of Natural History, Washington, D.C. 20560.** The prepublication price for individuals is $18.75, postage and handling included, until 31 March 1985 and $21.50 thereafter. Delivery of the Code will be in spring 1985. Checks drawn on a United States bank or International Money Orders should accompany all orders. Make checks payable to American Association for Zoological Nomenclature.

The American Ornithologists' Union solicits nominations for its **Brewster and Coues Awards**. Nominations and supporting materials should be sent to **Dr. Abbot S. Gaunt, Department of Zoology, The Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210-1293.** Materials must be received before **1 June 1985.**

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The **Frank M. Chapman Memorial Fund** gives grants in aid of ornithological research and also postdoctoral fellowships. While there is no restriction on who may apply, the Committee particularly welcomes and favors applications from graduate students; projects in game management and the medical sciences are seldom funded. **Applications are reviewed once a year and should be submitted no later than 15 January.** Application forms may be obtained from the **Frank M. Chapman Memorial Fund Committee, The American Museum of Natural History, Central Park West at 79th St., New York, New York 10024.**

Dr. David R. Wells was appointed Chapman Fellow for the period June 1984 through December 1984. He is working on an atlas of the distribution and speciation of oriental birds. Current Chapman Fellow Robert E. Bleiweiss has been granted an extension of his Fellow status through December 1984. He is studying systematics and speciation in Andean hummingbird genera.

Chapman grants during 1984, totalling $32,781 with a mean of $537, were awarded to: John G. T. Anderson, cooperative foraging behavior in the White Pelican; Ana Victoria Ayala, observations on the interaction between one species of hummingbird and the flowers it uses as food source in a sub-Andean forest; George Barrowclough, ornithological survey of avifauna of Cerro de la Neblina; Jonathan J. Becker, birds of the late Miocene Love Bone Bed local fauna; Henry Lawrie Bell, composition and foraging behavior of insectivorous birds in mixed-species flocks in montane forests of New Guinea; Robert I. Bowman, a genetic analysis of evolution in Galapagos finches; Charles R. Brown, costs and benefits of coloniality in Cliff Swallows (*Hirundo pyrrhonota*); Kenneth G. Bunch, bolus recovery by Gray Jays; Peter F. Cannell, systematics of the avian orders Coraciiformes and Piciformes and allies based on syringeal anatomy; William Carmen, evolution of noncooperative breeding in the California Scrub Jay (*Aphelocoma coerulescens californica*); John H. Carothers, microevolution of morphology in the Hawaiian Honeycreeper (*Vestiaria coccinea*); Ralph V. Cartar, can Red Phalarope chicks share post-hatching parental care?; Russell A. Charif, investigation of the function of song matching in mockingbirds (*Mimus polyglottos*); T. M. Crowe, phylogeny of the order Galliformes; C. R. Dickman, diet and prey selection of the Barn Owl in Malaysian oil palm plantations; Euan K. Dunn, census of Roseate Tern (*Sterna dougallii*) population on the Azores; Margaret Elowson-Haley, factors eliciting predator alarm calls in the Florida Scrub Jay; C. Craig Farquhar, breeding ecology of the White-tailed Hawk (*Buteo albicaudatus hypospodius*) in Texas; Peter Crawford Frederick, mating strategies in White Ibis (*Eudocimus albus*); Judy Gradwohl, population stability and rigid territoriality in some insectivorous birds on Barro Colorado Island; Rolf Karl-Heinz Grantsau, field guide to the birds of Brazil; Frederick Pearce Greene, determinants of guild structure among insectivorous birds in the Chiricahua Mountains, Arizona; John Morton Hagan III, colonial nesting in Ospreys; Thomas M. Haggerty, reproductive ecology of Bachman's Sparrow; Sylvia L. Halkin, use of song repertoires by male and female Northern Cardinals; J. Christopher Haney, selection pressures and the evolution of sociality in the White-throated Jay (*Cyanolyca mirabilis*); Russell A. Haughey, investigation of the role of the Western White-winged Dove (*Zenaida asiatica mearnsii*) in the pollination of the saguaro (*Cereus giganteus*); Paul Hendricks, foraging ecology of alpine Water Pipits; Holly H. Hobart, cytosystematics of some Arizona birds; Sylvia Hope, phylogeny of Corvidae; H. A. Isack, biology of the Greater Honeyguide (*Indicator indicator*) with emphasis on guiding behavior; Jan Kalina, socioecology of Black-and-white Casqued Hornbills and their role as seed disperser for tropical rain forest trees; Alan C.

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lengths (Feinsinger et al. 1979). If this proves to be the case, details on flight speeds would be needed to determine whether flight power considerations were involved in any way. The short wings of territorial hummingbirds (see Feinsinger and Chaplin 1975), for example, probably relate to the ability to accelerate and maneuver in chases and displays rather than to energetic considerations.

ACKNOWLEDGMENTS

I am especially grateful to C. H. Greenewalt, who prodded my thinking away from energetics and who made available unpublished analyses of hummingbird dimensions. R. Montgomerie, F. G. Stiles, and C. L. Gass generously provided access to unpublished manuscripts. P. Feinsinger, C. L. Gass, F. R. Hainsworth, J. P. Myers, and L. L. Wolf criticized early drafts of this paper. R. Ray, A. Mack, D. Wechsler, F. Joyce, P. Marcotullio, and D. Emery assisted in the field. I am indebted also to the staff of the Servicio de Parques Nacionales of Costa Rica for their many courtesies and their assistance in Parque Corcovado. I extend special thanks to A. Ugalde, F. Cortez, J. Gamboa, H. Delgado, and M. Felis.

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Nominations for Elective Members and Fellows of the A.O.U. may be made up until 5 months prior to the next stated meeting. Nominations of Fellows must be signed by three Fellows. Nominations of Elective Members must be signed by three Fellows or Elective Members. The number of Fellows under 60 years of age is restricted to 75 by the bylaws. However, the number of new Elective Members each year is in large part determined by the number nominated—we can elect up to 75% of the nominees. Prescribed forms may be obtained from the Secretary (see inside front cover of *The Auk* for address). Completed forms must be returned to the Secretary by **7 May 1985** in order to be eligible.

Nominations for officers may be made in writing to the Secretary at any time prior to the next meeting of Fellows and Elective Members, which is 7 October 1985. The following positions will be vacant in 1985: Vice President and three Elective Councilors.

MILLER, K. J. 1976. Gut morphology of Mallards in relation to diet. J. Wildl. Mgmt. 39: 168-173.

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