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INTRASEASONAL REPRODUCTIVE COSTS FOR THE HOUSE SPARROW (*PASSER DOMESTICUS*)

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ABSTRACT.—House Sparrows (*Passer domesticus*) near Calgary, Alberta begin breeding in early spring and continue through to late summer. High productivity from previous broods is negatively correlated with fledgling production from second and third broods. Although fat reserves may limit the ability of females to raise young, there is no concomitant drop in clutch size or in the probability of renesting. Pairs that fledge many young in a year space fledgling production evenly over the breeding season but are most productive in mid-season. The interval between fledging and the initiation of the next clutch increases with the number fledged. This delay, an indication of the physiological strain involved in rearing young, is greater for later broods and for females nesting in trees. Measures of reproductive effort (clutch size, number fledged, length of the nestling period) vary seasonally but give no indication of peaking for last broods. Thus, reproductive effort is not adjusted to parallel changes in the probability of surviving to the next breeding attempt. *Received 3 November 1981, accepted 24 April 1982.*

A COMMON assumption underlying theoretical discussions of life-history phenomena is that trade-offs in life-history characteristics occur (Williams 1966, Charnov and Krebs 1974, Stearns 1976, Snell and King 1977). For example, Pianka and Parker (1975) partition the reproductive value of an individual of age X in a stable nongrowing population into fecundity at age X and expected fecundity conditioned by survival to ages $X + 1, X + 2, \dots, X + N$. Clearly if survivorship is lowered by current reproduction, future fecundity is reduced.

Many researchers of life-history phenomena in birds have investigated whether or not the modal clutch size is the most productive, as predicted by Lack (1947, 1966). If productivity is measured as the number of young fledged from a brood, then clutch sizes larger than modal appear to be optimal (Klomp 1970, von Haartman 1971, Jones and Ward 1976, Murphy 1978). If parental survivorship is reduced by the effort of raising a large brood, however, then the optimal clutch size might be lower than the most productive (Fisher 1930, Charnov and Krebs 1974). Studies testing the relationship between brood size and parental survivorship show equivocal results. Bryant (1979) found a reduction in the overwinter survivorship of double-brooded female House Martins (*Delichon urbica*), and male Pied Flycatchers (*Ficedula hypoleuca*) feeding many young were less likely to return to the study area than those feeding fewer young (Askenmo 1979). Lack (1966) and Kluyver (1970) present evidence suggesting an inverse relationship between brood size and parental survivorship. De Steven (1980), however, did not find a reduction in the survivorship of female Tree Swallows (*Iridoprocne bicolor*) as a result of brood enlargement. Smith (1981), after demonstrating a positive association between reproductive effort and survivorship, concluded that a trade-off between fecundity and survivorship should not be assumed for passerine birds.

The longevity and mobility of birds usually prevents a precise determination of mortality rates for individuals with a known reproductive history. If dispersers are a nonrandom sample of the population (Lowther 1979), then estimates of survivorship based on individuals staying at or returning to the study area will be biased. As a consequence, the effect of reproduction on survivorship is often estimated from physiological evidence. Weight losses for females through the breeding season suggest a physiological strain that may reduce survivorship (Newton 1966, Hussell 1972, Bryant 1979). For female House Sparrows (*Passer domesticus*), Pinowska (1979) has shown that levels of fat influence clutch size, while lean dry weight (an indicator of protein level) may determine the number of broods raised in a season. Norberg

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(1981) presented the hypothesis that adult weight losses during breeding may be adaptive. This would be true if the reduced cost of collecting food for the nestlings increases fledgling numbers more than it reduces survivorship and future fecundity.

Birds that raise more than one brood in a season may be expected to show differential reproductive effort and productivity through the breeding season. There is a higher probability of surviving from one brood to the next during the breeding season than from the last brood of one season to the following spring. An increase in the level of reproductive effort would be expected as the probability of surviving to the next breeding attempt decreases. There is some evidence that high levels of reproductive effort lower the ability of females to invest in a subsequent brood. For Great Tits (*Parus major*), Kluyver (1963) found a lesser probability of a second brood if the first was large. Pinkowski (1977) noted a drop in the clutch size of second broods for Eastern Bluebirds (*Sialia sialis*) that raised a large first brood, and Smith and Roff (1980) found that an increase in the interbrood interval was associated with a large first brood for Song Sparrows (*Melospiza melodia*).

In this study I look at the productivity of multibrooded House Sparrows through the breeding season and address two questions. First, is there variation in the productivity of successive broods within the breeding season associated with brood size in earlier broods (is there a demonstrable within-season cost associated with reproduction)? Second, do adults modify their reproductive effort in accordance with seasonal changes in the probability of renesting and surviving?

METHODS AND MATERIALS

Study site.—In 1977, the study areas were six farms near Conrich, Alberta, 5 km east of Calgary. For 1978, all data were collected at one of these farms, 8 km east of Calgary. At each of the farms, about 20 nest boxes were erected in fall 1974 (see Murphy 1978 for details). As well as nesting in boxes, the sparrows used buildings, machinery, and trees. At the farm studied both years, nests built in trees were monitored in addition to those in nest boxes.

Data collection.—Nests were inspected at 3–5 day intervals from 2 May to 15 August 1977 and from 20 April to 13 August 1978. If weather conditions permitted, a 3-day interval was maintained. Eggs were counted and numbered. Nestlings 5–6 days old were banded with a U.S. Fish and Wildlife Service aluminum leg band and color marked with leg bands after reaching a 20-g weight.

Data analysis.—Because the nests were not checked every day, exact clutch-initiation data and nestling ages were not known for all nests. For these cases, estimates were used. Nestling age when first found was estimated by comparing the weight of the largest nestling in a brood to average values obtained from broods of known age. Clutch-initiation date was estimated by assuming an average incubation period of 11 days and a laying rate of one egg per day (McGillivray 1978). This estimate was needed only for clutches begun before my arrival at the study area.

In this study I investigated the productivity from multiple broods of a pair; hence, I made the general assumption that broods raised at a single nest through the breeding season were raised by the same pair. House Sparrows usually remain at the same site unless one of the pair dies (Summers-Smith 1963). To reduce the importance of this potential source of error, I imposed some residency conditions. If a tree nest was extensively modified following a nesting attempt, I assumed that a new pair was nesting. The average interval between successive clutch initiations for first through third clutches for each brood size was determined. Ninety five percent prediction intervals were calculated for each clutch-interval, brood-size combination. Nests where the interclutch interval fell outside these limits were excluded from further analyses.

The interval between the departure of the last nestling and the initiation of the next clutch is called the interbrood interval. The date of fledgling departure was considered to be the midpoint of the interval between the last observation of the nestlings and the first nest check after departure. Fledging is a gradual process, so a departure date is only an approximate measure. Paired comparison *t*-tests were used to compare the mean interbrood interval of successive broods and different nest types.

For the investigation of the effects of one brood on the next breeding attempt, data for the two years were pooled. Pooling requires trends to be consistent over the two years in order for the trends to be detected, and productivity for both years was similar except for the first broods. The strength of trends associated with brood size was measured by Pearson's product-moment correlation coefficient, r. Although significance levels were determined for r, paired variables were not tested for bivariate normality. Nonetheless, r is a useful indicator of trend.

This analysis assumes that fledglings of equal weight contribute equally to parental fitness. This assumption may not be valid for a species with a long breeding season. Dyer et al. (1977) published the following survivorship equation for juvenile House Sparrows (from Summers-Smith 1963); $Y =$

TABLE 1. Seasonal variation in productivity: comparison between years; yearly means with standard error.

Variable	Clutch							
	First		Second		Third		Fourth	
	1977	1978	1977	1978	1977	1978	1977	1978
Sample size	276	210	227	157	162	87	40	15
Clutch initiation date[a]	131.8	133.8	157.1	162.5	183.1	191.2	198.6	206.2
Clutch size	4.8 (0.06)	4.8 (0.06)	5.2 (0.06)	5.0 (0.07)	4.8 (0.07)	4.8 (0.11)	4.3 (0.17)	4.5 (0.13)
Number hatching	3.0 (0.10)	2.8 (0.14)	3.0 (0.12)	3.2 (0.14)	2.5 (0.15)	3.1 (0.19)	2.1 (0.26)	2.4 (0.40)
Number fledging[b]	1.8 (0.10)	1.0 (0.10)	1.9 (0.08)	1.8 (0.13)	1.5 (0.14)	1.5 (0.18)	0.8 (0.19)	0.8 (0.34)
Fledging weight (g)[c]	24.1 (0.20)	26.1 (0.30)	25.3 (0.27)	26.6 (0.25)	26.1 (0.28)	27.1 (0.36)	27.0 (0.56)	24.0 (0.98)

[a] Date measured from the beginning of the year.
[b] Significantly different between years for first broods ($P < 0.05$, t-test).
[c] Significantly different between years for all broods ($P < 0.05$, t-test).

TABLE 2. Interbrood interval (days).

Number of fledglings	1978	1977-box nests[a]	1977-tree nests[a]
		First to second	
0	11.4	6.0**	8.1*
1	6.4	6.3	8.0
2	7.4	7.3	8.3
3	10.8	8.0	9.4
4	9.5	9.1	11.0
5	11.0	8.3	—
		Second to third	
0	10.7	6.9**	7.2
1	10.0	7.4	9.2
2	10.9	7.9	9.4
3	11.7	8.7	10.0
4	10.2	8.1	9.2
5	12.0	10.6	9.5

[a] * = correlation with number of fledglings is significant at $P < 0.05$.
** = correlation with number of fledglings is significant at $P < 0.01$.
Paired comparison t-test for differences between first to second and second to third intervals: $d = 0.694$, $t = 1.92$, 16 df, $0.05 < P < 0.10$.
Paired comparison t-test for differences between tree and box nests for 1977: $d = 1.18$, $t = 4.32$, 10 df, $P < 0.01$.

$102.9X^{-0.688}$, where Y = percentage of juveniles surviving and X = month after fledging. If this equation accurately describes juvenile survivorship, then late-fledging young are more likely to be recruited into the population, and reproductive effort should be concentrated toward the end of the breeding season. In a seasonal environment such as that at Calgary, however, late-fledging young experience cold temperatures, snowcover, and food shortages at a younger age than do early-fledging young. Thus, a late-fledging cohort might suffer greater overwinter mortality (McGillivray 1981a).

Predation on eggs and nestlings was rare at this site. Few entire clutches or broods disappeared, and most nesting mortality can be attributed to starvation.

RESULTS

For species that raise a single brood each season, the breeding season would be that period of the year during which parents have the highest probability of successfully fledging young. The same is true for a multibrooded species, but conditions are unlikely to be constant through the season. The average House Sparrow productivity for clutch initiations 1 through 4 is displayed in Table 1. If one considers only the average number fledged, the second brood is the most productive, the third slightly less, the fourth relatively unproductive, and the first quite different between years.

TABLE 3. Relationship between fledgling production and measures of reproductive effort (and standard error) for each brood.

Number fledged	Clutch size[a]	Fledgling weight	Nestling period length (days)[a]	Breeding attempt length (days)[a,b]
		Brood 1		
0	4.68** (0.06)	—	2.82* (0.25)	26.32** (0.60)
1	4.81 (0.17)	24.52 (0.48)	13.03 (0.50)	33.32 (0.55)
2	4.50 (0.13)	25.47 (0.35)	13.56 (0.41)	35.73 (0.31)
3	4.87 (0.10)	25.21 (0.36)	13.58 (0.28)	36.65 (0.52)
4	5.29 (0.11)	24.30 (0.39)	13.77 (0.36)	37.23 (0.55)
5	5.58 (0.15)	23.74 (0.45)	13.91 (0.72)	37.80 (1.08)
6	6.00 (0.00)	27.84 (0.00)	15.00 (0.00)	39.00 (0.00)
		Brood 2		
0	4.95** (0.08)	—	2.28* (0.27)	24.00** (0.88)
1	4.96 (0.19)	25.78 (0.64)	12.41 (0.55)	33.94 (0.84)
2	5.13 (0.11)	26.57 (0.36)	12.31 (0.30)	35.72 (0.66)
3	5.20 (0.09)	26.17 (0.35)	12.90 (0.26)	37.46 (0.56)
4	5.37 (0.10)	25.07 (0.38)	12.76 (0.52)	36.03 (0.51)
5	5.45 (0.11)	24.96 (0.63)	13.23 (0.50)	39.03 (0.98)
6	6.00 (0.00)	25.75 (3.50)	14.50 (2.50)	43.00 (0.00)
		Brood 3		
0	4.59* (0.10)	—	2.06 (0.27)	23.44 (1.03)
1	5.00 (0.25)	26.20 (0.83)	12.08 (0.57)	37.00 (3.50)
2	4.50 (0.19)	26.64 (0.52)	11.74 (0.51)	—[c]
3	4.89 (0.14)	26.80 (0.42)	11.97 (0.32)	37.25 (1.70)
4	5.19 (0.09)	26.77 (0.41)	12.67 (0.32)	35.80 (1.96)
5	5.25 (0.11)	26.05 (0.58)	12.57 (0.80)	33.60 (0.68)
6	6.00 (0.00)	25.42 (0.00)	13.00 (0.00)	—[c]
		Brood 4		
0	4.22 (0.17)	—	1.87 (0.50)	—[c]
1	4.67 (0.42)	26.65 (0.83)	10.67 (1.10)	—
2	4.20 (0.26)	24.76 (1.74)	10.50 (0.87)	—
3	4.80 (0.37)	27.60 (0.72)	11.80 (0.58)	—
4	5.00 (0.00)	24.31 (1.31)	13.50 (1.50)	—

[a] * = correlation with the number of fledglings significant at $P < 0.05$.
** = correlation with the number of fledglings significant at $P < 0.01$.
[b] Interval between successive clutch initiations.
[c] No subsequent clutch initiated.

High fledgling output from first broods is unusual for House Sparrows in this area (Murphy 1977), because cold weather, rain and snow are common throughout May (McGillivray 1981b).

That the interval between the fledging of a brood and the initiation of the next clutch (interbrood interval) increases as the number fledging increases is shown in Table 2. The longer interval between second and third broods compared to the interval between first and second broods implies that the physiological costs of breeding are cumulative. Sample sizes for the third to fourth brood interval are too small to consider (<5), except for box nests in 1977 that fledged no young in the third brood (interbrood interval = 7.6 days, $n = 17$), where an increase over the second to third interval is observed. The longer interbrood interval for pairs nesting in trees suggests that daily energy requirements are lower for box-nesting females.

Why the physiological cost of nesting might increase with the number of young fledged from a brood is shown in Table 3. On the average, females must expend energy laying additional eggs, and the pair must spend a longer time feeding the young in large broods. As brood size increases, adult House Sparrows increase the rate of feeding trips to the nestlings (Summers-Smith 1963, Seel 1969, Sappington 1975, McGillivray 1981a), and, at least for these two years, average fledging weight does not change

TABLE 4. Relationship between the number of fledglings produced and productivity in the subsequent breeding attempt.

Number fledged	n	Clutch size	Number fledged	Probability of starting next clutch
Brood 1		**Brood 2**		
0	234	5.10	1.69	0.70
1	38	5.48	2.36	0.82
2	61	5.21	2.23	0.77
3	81	5.06	2.07	0.84
4	56	5.10	1.88	0.73
5	14	5.40	1.60	0.71
6	1	4.00	0.00	1.00
Brood 1 and Brood 2		**Brood 3**		
0	41	4.63	1.22	0.60
1	13	5.08	1.69	0.81
2–3	75	4.84	1.83	0.75
4–5	65	4.83	1.54	0.69
6–7	37	4.51	1.46	0.51
8–9	12	5.00	0.50	0.75
>9	1	5.00	0.00	1.00
Broods 1, 2, and 3		**Brood 4**		
0	7	4.00	1.14	0.22
1–3	18	4.78	0.50	0.41
4–6	20	4.20	1.00	0.22
7–9	8	4.25	0.62	0.15
10–12	2	4.00	0.50	0.15

with brood size. Although thermoregulatory costs should be lower for nestlings in larger broods, these are unlikely to offset the extra feeding demands on parents created by more nestlings.

For the combined breeding seasons 1977 and 1978, pairs that showed higher productivity from the first clutch tended to have lower output from the second clutch (Table 4). For pairs that fledged at least one young from the first brood, there is a negative correlation between the number fledged in brood 1 and the number fledged in brood 2 ($r = -0.85$, 4 df, $P < 0.05$). The class containing pairs fledging no young was excluded from analyses because of its heterogeneity. It includes a range from pairs raising young to near fledging to others losing clutches before hatching. The probability of starting a second clutch and the size of second clutches are uncorrelated with the number of fledglings from brood one.

Because the interbrood interval data suggested that physiological strain is additive over broods, I compared third and fourth brood productivity with summed fledgling totals from all previous broods. For pairs fledging at least one young, the summed fledgling production from broods 1 and 2 is negatively correlated with the number fledging in brood 3 (Table 4, $r = -0.81$, 4 df, $0.05 < P < 0.10$). Again, the probability of renesting and the average clutch size are not related to productivity earlier in the season.

TABLE 5. Modal number fledged in each brood for pairs grouped by seasonal total fledgling production.

	Seasonal total fledgling production					
Brood	1–2	3–4	5–6	7–8	9–10	>10
1	2.0	3.0	3.0	3.5	3.0	3.0
2	2.0	3.0	3.0	4.0	5.0	4.5
3	0.0	0.0	0.0	0.0	4.5	4.0
4	0.0	0.0	0.0	0.0	1.5	1.5

There is a nonsignificant, negative relationship between total productivity in broods 1, 2, and 3 and the average number fledging in brood 4 (Table 4). The probability of initiating a subsequent brood has dropped from the previous two comparisons and is lowest for pairs with the highest fledgling numbers from the previous three broods.

When the fledgling data from the three comparisons (broods 1 vs. 2; 1 and 2 vs. 3; and 1, 2, and 3 vs. 4) are combined and standardized by transformation to Z-scores, previous productivity is shown to be negatively correlated with future productivity ($r = -0.63$, 14 df, $P < 0.05$).

The strong negative relationship between first and second brood productivity is reflected in the distribution of fledgling production over the breeding season. Table 5 demonstrates that the highest fledgling totals were achieved by pairs with high post-first-brood productivity.

A prediction from life-history theory is that, unless the raising of last broods lowers adult survivorship, reproductive effort should be higher for that brood than for broods earlier in the season. Last broods, as defined here, include fourth broods and third broods after which no fourth clutch was initiated. Because no physiological measures were made, only indirect estimates of effort can be used. Table 6 demonstrates that, for four possible indicators

TABLE 6. Measures of reproductive effort (and standard error) by pairs for broods after which fourth clutches were initiated, third broods that were last broods and fourth broods.

Variable	Third broods: Not last	Third broods: Last	Fourth broods
Clutch size	4.83 (0.10)	4.74 (0.07)	4.36 (0.13)
Number fledged	2.93 (0.18)	2.78 (0.13)	2.11 (0.23)
Fledgling weight (g)	26.54 (0.40)	26.48 (0.25)	26.01 (0.65)
Nestling period (days)	12.36 (0.37)	11.70 (0.25)	11.22 (0.48)

of reproductive effort, average values for third broods that are also last broods are not significantly different from those of third broods after which a fourth clutch was laid. There is also no evidence of enhanced effort for fourth broods.

DISCUSSION

These data suggest that the trade-offs and the theory required to account for them are different for single and multibrooded species. An inverse relationship between present and future fecundity is suggested but not as a function of reduced survivorship. Rather, high productivity delays the initiation of the following clutch and is negatively correlated with productivity from future clutches.

Two studies (Schifferli 1976, Pinowska 1979) have monitored the physiological condition of adult House Sparrows through the breeding season. For females, fat level drops during egg laying, is partially replaced during incubation, drops again during the nestling period, and presumably is restored in the interbrood interval. Protein level drops gradually through the breeding season. Pinowska (1979) found that clutch size was correlated with fat level and the number of clutches initiated in a season was limited by protein level. For males, fat level drops during the nestling period and is replenished in the interbrood interval.

These two studies suggest that, after completing a brood, both sexes of a pair fledging many young would have lower fat levels than those of a pair fledging few young. The lower fat level should result in either a smaller clutch size or a longer delay in the initiation of the subsequent clutch. My observations show that clutch size is not affected by previous productivity but subsequent clutch initiations are delayed. The longer interval between second and third broods compared to that between first and second broods indicates a cumulative physiological effect of the first two broods. This effect is suggested by Pinowska's observations (1979) of protein levels and by the reduced survivorship of double-brooded House Martins found by Bryant (1979).

The longer interbrood interval for pairs using tree nests supports other observations (Murphy 1978, McGillivray 1981b) showing that box nests are superior nest sites. A warmer microclimate (Mertens 1977) would reduce nestling thermoregulatory costs, and a reduction in the need for nest maintenance would facilitate renesting in boxes.

While the tree-versus box-nest comparisons provide appealing evidence for physiological correlates of reproductive costs, they point out a problem in the evaluation of reproductive effort. If nest-site selection can modify the cost of raising young, then other factors such as weather, distance to food sources, time of clutch initiation, and parental age and size are also likely to modify the reproductive effort associated with raising a brood of fixed size. The importance of factors other than productivity may provide a partial explanation for the contradictory results obtained in previous studies of the trade-off between reproductive effort and survivorship in passerines (Bryant 1979, Askenmo 1979, De Steven 1980, Smith 1981).

There is no simple physiological hypothesis to account for reduced productivity from pairs fledging many young. Because clutch size and the probability of renesting are generally unrelated to previous productivity, the cost of reproduction is felt by parents during the incubation and nestling period. While the nestling period is considered highly demanding (Ricklefs 1973), much of the evidence (particularly weight losses for adults) is now questionable (Norberg 1981).

There is no evidence from the data that reproductive effort increases as the probability of surviving to the next breeding attempt decreases. As mentioned earlier, however, only partial estimates of reproductive effort are possible. Pinowska (1979) felt that breeding in House Sparrows followed a cyclical pattern in which a pool of resources is alternatively tapped and partially replenished until depleted below a critical point and breeding ceases. Hence, second, third, and fourth broods are initiated only by females that possess sufficient resources. Last broods, which should show enhanced reproductive effort according to life-history theory, might, in fact, show evidence of physiological strain. Seasonal differences make comparisons among broods difficult to interpret, but the comparison between third broods that were last broods and third broods after which a fourth clutch was initiated is revealing. Table 6 indicates that, while none of the chosen measures of effort is different between groups, the direction of difference always suggests lower resource levels for pairs raising last broods.

A reviewer pointed out that life-history theorists consider ultimate causes, but field workers are forced to explain proximate reasons for phenomena such as clutch size, number of breeding attempts per season, and survivorship. The lack of concordance between theory and field observations (Smith 1981, this study), while perhaps an indictment of the theory, is equally likely to be the result of failure to control and account for proximate variation.

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World Inventory of Avian Skeletal Specimens. 1982. D. Scott Wood, Richard L. Zusi, and Marion Anne Jenkinson.
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GENIC VARIATION, SYSTEMATIC, AND BIOGEOGRAPHIC RELATIONSHIPS OF SOME GALLIFORM BIRDS

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ABSTRACT.—Starch gel electrophoresis was used to evaluate levels and patterns of genic differentiation among 10 species of galliform birds in the Phasianidae (9) and Tetraonidae (1). The phasianids included an Old World quail, a partridge, a pheasant, and six species of New World quail. Measures of within-species genetic variation included heterozygosity, percentage polymorphic loci, and number of alleles per polymorphic locus. These values were similar to but lower than those reported for other birds. Genetic distances among conspecific populations and among congeneric species were low compared to other avian results. Genetic distances among noncongeners both within and between families were considerably higher, however, than those reported for passerine birds. Thus, more studies of levels of genic differentiation among nonpasserines are required to complement the literature on genic divergence among passerines and to enable us to make general statements about genic evolution in birds.

Phenograms and phylogenetic trees suggested that *Phasianus colchicus, Tympanuchus pallidicinctus, Coturnix coturnix, Alectoris chukar,* and the New World quail (Odontophorinae) are genically distinct taxa. The branching sequence among the non-Odontophorine taxa is unresolved by our data. The branching order among taxa in the Odontophorinae from a common ancestor is: *Cyrtonyx montezumae, Oreortyx pictus, Colinus virginianus, Callipepla squamata, Lophortyx gambelii,* and *L. californicus.* The genera *Cyrtonyx, Oreortyx,* and *Colinus* are clearly distinct from *Callipepla* and *Lophortyx,* which are quite similar to each other genically.

We use a fossil species from the mid-Miocene of Nebraska to calibrate our genetic distances. We estimate dates of divergence of taxa in the Odontophorinae and offer a hypothesis on their historical biogeography. Our analysis suggests that three east–west range disjunctions could account for the origin of *Oreortyx* (12.6 MYBP), *Colinus* (7.0 MYBP), and *Callipepla-Lophortyx* (2.8 MYBP). We suggest that *L. californicus* and *L. gambelii* should be considered distinct species because of an apparent lack of panmixia in zones of sympatry, even though the *D* between them is typical of that found between subspecies of other birds. *Oreortyx* and *Colinus* should remain as distinct genera, while our data are equivocal on the status of *Callipepla* and *Lophortyx.*[3] *Received 9 March 1982, accepted 5 July 1982.*

ALLOZYME electrophoresis has been used less frequently to examine genetic variation within and among groups of birds than in other vertebrates (see review in Nevo 1978). Some workers have examined patterns of intraspecific genic variation in passerines (e.g. Barrowclough 1980, Johnson and Brown 1980, Corbin 1981, and references therein), and a few have examined avian intrafamilial relationships (e.g. Barrowclough and Corbin 1978, Avise et al. 1980a–c). They have found that passerine birds possess considerably lower levels of genic (= allozymic) differentiation than other vertebrate taxa, at comparable taxonomic levels.

Several workers have compared the level of genic divergence and taxonomic rank for various vertebrate and invertebrate taxa (e.g. Ayala 1975, Avise et al. 1980b). Barrowclough et al. (1981) present similar data for birds but discuss reasons why comparisons across different groups of organisms may be inappropriate; these include taxonomic artifacts [e.g. avian, mammalian, and reptilian genera may not be comparable because of the way in which taxonomists partition variation (Sibley and Ahl-

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[3] *Lophortyx* has been merged with *Callipepla* in the Thirty-fourth Supplement to the American Ornithologists' Union check-list of North American Birds [Auk 99 (3, Suppl.): 5CC].

quist 1982)] and differences in rates of evolution, mating systems, effective population sizes, recency of common ancestry, and dispersal parameters. Whether or not low levels of genic divergence typify birds as a group is unclear, because only Barrowclough et al. (1981) studied a nonpasserine taxon. They found higher levels of differentiation among some procellariiform taxa than those usually found among passerines. Because the levels of genetic differentiation are sometimes used to make inferences about evolutionary processes (Avise et al. 1980c, Templeton 1980), we clearly need additional studies of nonpasserines before we can make general statements about genic evolution in birds.

The patterns of genic differences can also be used to infer phylogenetic relationships (e.g. Barrowclough and Corbin 1978, Zink 1982). In this paper we examine levels of genic variation and phylogenetic relationships among 10 species from 5 of 10 genera of New World quail, an Old World quail, a partridge, a pheasant, and a grouse. We use our phylogenetic hypothesis to construct an estimate of the evolutionary history of some New World quail. We also evaluate previous statements about the taxonomic relationships of these galliform birds.

Materials and Methods

We examined 217 specimens of galliform birds representing 10 species. Species, localities, sample sizes, and the taxonomic framework used in this paper are given in Appendix 1. Nomenclature follows the A.O.U. check-list (1957, 1973).

Liver, heart, and kidney tissue were excised in the field within 4 h of death and frozen in liquid nitrogen. Tissues were homogenized using the methods of Selander et al. (1971), and extracts were stored at −76°C until used for electrophoresis. Combined tissue extracts were subjected to horizontal starch gel electrophoresis as described by Selander et al. (1971). Gel and buffer systems for the loci listed in Appendix 2 were essentially the same as those described by Yang and Patton (1981). More detailed information regarding electrophoretic conditions is available from the authors.

We assume that our electrophoretically detectable variants (= electromorphs) at a locus differ genetically; hence, we refer to them as alleles. Alleles at a locus were coded by their mobility from the origin. The most anodal allele was designated as a, with slower alleles denoted as b, c, d, etc. Isozyme nomenclature follows Yang and Patton (1981). Heterozygosity ($\bar{H}$) was defined as the number of heterozygous genotypes recorded in a sample divided by the product of the number of loci and the number of individuals assayed (see Corbin 1981 for a discussion of calculating $\bar{H}$). Estimates of percentage polymorphism were based on the number of loci having more than one allele divided by the total number of loci (27) examined.

The measures of Nei (1978) and Rogers (1972) were used to estimate genetic distances between taxa. Cluster analyses, summarizing the matrix of Rogers' D-values, were performed with both the unweighted and weighted pair-group methods, using arithmetic means (UPGMA and WPGMA, respectively). The cophenetic correlation coefficient, r_{cc}, was used to evaluate how well the resultant phenograms represent the original distance matrix. Sneath and Sokal (1973) provide details on these phenetic methods. Phylogenetic trees, also based on Rogers' D-values, were constructed according to the methods of Farris (1972; Wagner trees) and Fitch and Margoliash (1967; F-M trees). The Wagner tree is an approximation of the most parsimonious tree. The F-M procedure constructs a number of trees by altering the branching structure and branch lengths. Alternative trees were evaluated by the percentage standard deviation (%SD) and by the number of negative branches (the fewer the better). A lower %SD means a better fit of distances implied by the tree to the original distance matrix (Fitch and Margoliash 1967). A cladistic analysis, *sensu* Hennig (1966), using alleles as character states (see Wake 1981), basically corroborated the above methods. The allele in *T. pallidicinctus* (Tetraonidae) was considered "primitive" when comparing the pattern of allele distribution in the remaining taxa (Phasianidae), i.e. *T. pallidicinctus* was used as an "outgroup" to the phasianids.

Results

Protein variation.—Twenty structural proteins and enzymes encoded by 27 presumptive genetic loci were examined in all individuals. Allelic frequencies for the 23 variable loci, percentage polymorphism and heterozygosity, and number of alleles per polymorphic locus are given in Appendix 2. Four loci (Mdh-1, Mdh-2, Lap, Pt-1) were monomorphic and fixed for the same electromorph across species. Seven loci (αGpd-1, Got-2, Udh, Gdh, Ldh-1, Ldh-2, Pept-2) were monomorphic within species but exhibited interspecific differences. The remaining loci were polymorphic in some species and also showed interspecific fixed differences.

We exclude the laboratory strains of *Coturnix* and *Alectoris* from discussions of within-species variation, because these levels of variation may

TABLE 1. Matrix of genetic distances between 17 taxa of galliform birds. Distances computed by methods of Nei (1978) above diagonal and Rogers (1972) below diagonal.

	Species						
Species	1	2	3	4	5	6	7
1. *Tympanuchus pallidicinctus*	—	1.041	1.308	1.291	1.326	1.201	1.483
2. *Phasianus colchicus*	0.649	—	1.446	1.282	1.310	1.172	1.654
3. *Coturnix coturnix* A	0.721	0.749	—	0.064	0.059	1.185	1.340
4. *C. coturnix* B	0.713	0.714	0.109	—	0.056	1.136	1.209
5. *C. coturnix* C	0.729	0.721	0.086	0.101	—	1.190	1.346
6. *Alectoris chukar*	0.695	0.682	0.685	0.665	0.689	—	0.962
7. *Lophortyx gambelii*	0.769	0.799	0.725	0.692	0.730	0.616	—
8. *L. californicus* A	0.773	0.797	0.728	0.690	0.730	0.617	0.028
9. *L. californicus* B	0.774	0.801	0.732	0.694	0.734	0.617	0.032
10. *L. californicus* C	0.768	0.795	0.727	0.688	0.728	0.610	0.037
11. *Callipepla squamata* A	0.773	0.758	0.752	0.727	0.761	0.652	0.106
12. *C. squamata* B	0.764	0.750	0.742	0.720	0.752	0.644	0.106
13. *Colinus virginianus* A	0.770	0.732	0.741	0.741	0.753	0.687	0.262
14. *C. virginianus* B	0.772	0.729	0.739	0.738	0.751	0.687	0.262
15. *Oreortyx pictus*	0.808	0.764	0.751	0.744	0.760	0.649	0.348
16. *Cyrtonyx montezumae* A	0.744	0.731	0.746	0.737	0.754	0.684	0.497
17. *C. montezumae* B	0.735	0.727	0.742	0.734	0.751	0.680	0.492

TABLE 1. Continued.

	Species									
Species	8	9	10	11	12	13	14	15	16	17
1. *Tympanuchus pallidicinctus*	1.495	1.495	1.475	1.493	1.476	1.487	1.495	1.668	1.364	1.335
2. *Phasianus colchicus*	1.627	1.646	1.617	1.430	1.419	1.342	1.331	1.476	1.334	1.326
3. *Coturnix coturnix* A	1.340	1.343	1.330	1.448	1.429	1.393	1.389	1.450	1.416	1.407
4. *C. coturnix* B	1.204	1.216	1.192	1.339	1.345	1.423	1.413	1.433	1.399	1.390
5. *C. coturnix* C	1.327	1.335	1.312	1.467	1.449	1.427	1.421	1.468	1.435	1.425
6. *Alectoris chukar*	0.967	0.966	0.947	1.071	1.054	1.184	1.189	1.056	1.170	1.158
7. *Lophortyx gambelii*	0.005	0.007	0.008	0.089	0.082	0.295	0.295	0.410	0.671	0.653
8. *L. californicus* A	—	0.000	0.000	0.115	0.100	0.301	0.298	0.418	0.640	0.624
9. *L. californicus* B	0.013	—	0.000	0.121	0.102	0.306	0.304	0.421	0.634	0.617
10. *L. californicus* C	0.019	0.015	—	0.120	0.103	0.308	0.306	0.431	0.641	0.623
11. *Callipepla squamata* A	0.129	0.130	0.131	—	0.003	0.258	0.262	0.491	0.664	0.645
12. *C. squamata* B	0.125	0.117	0.126	0.022	—	0.241	0.244	0.473	0.613	0.593
13. *Colinus virginianus* A	0.274	0.276	0.280	0.244	0.229	—	−0.002	0.538	0.478	0.462
14. *C. virginianus* B	0.273	0.277	0.283	0.252	0.237	0.015	—	0.540	0.463	0.448
15. *Oreortyx pictus*	0.355	0.354	0.367	0.400	0.391	0.424	0.427	—	0.746	0.744
16. *Cyrtonyx montezumae* A	0.479	0.476	0.479	0.493	0.473	0.395	0.385	0.533	—	0.001
17. *C. montezumae* B	0.476	0.472	0.472	0.483	0.463	0.389	0.383	0.533	0.018	—

have been affected by prolonged captivity. The average proportion of polymorphic loci for the wild species is 14.5% (range 0–29.6%). $\bar{H}$ is 2.6% and ranges from 0 to 5.1% (Appendix 2). The values of $\bar{H}$, percentage polymorphic loci, and number of alleles per polymorphic locus are similar to but lower than those reported for other groups of birds (Barrowclough and Corbin 1978, Avise et al. 1980a, Zink 1982).

Interspecific genetic distance.—The matrix of genetic distances between taxa is given in Table 1. A summary (Table 2) of genetic distance as a function of various taxonomic groupings shows that $\bar{D}$ increases as taxonomic groupings become more inclusive, at least to the subfamily level. This suggests that the taxonomic groupings are "biologically real," based on our genetic analysis. Levels of $\bar{D}$ for other avian taxa are also shown in Table 2 for comparison with the galliform $\bar{D}$'s.

At the local population level, the galliforms sampled here show less differentiation ($\bar{D}$ =

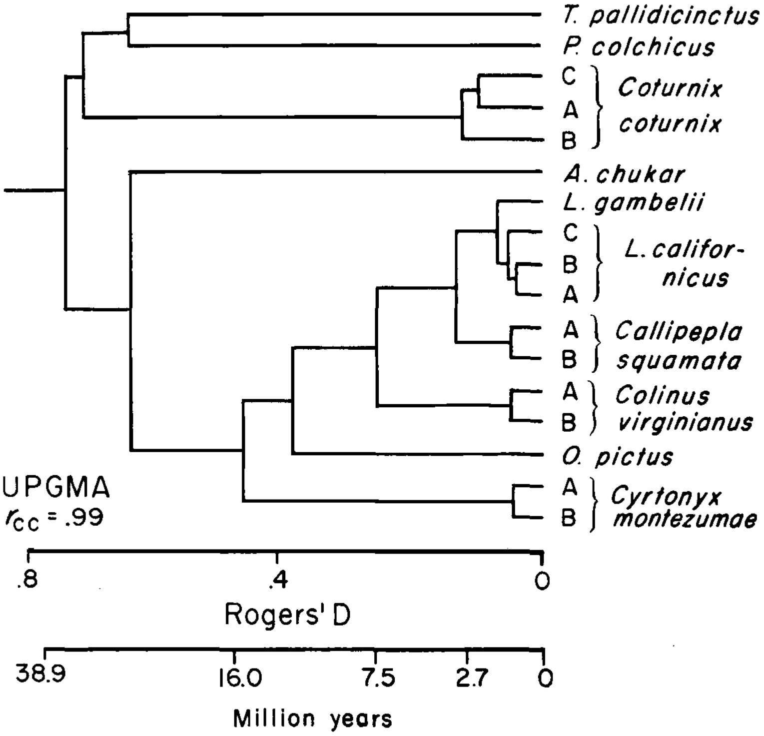

Fig. 1. UPGMA phenogram derived from the matrix of Rogers' D-values (Table 1). Geographic localities given in Appendix 1. Time scale determined from the formula $t = 26.3 \times 10^6 D$; see text.

0.0007) than other birds, although this may be due to the close proximity of some of the samples (Appendix 1). The $\bar{D}$-value between *L. gambelii* and *L. californicus*, 0.0067, is similar to that observed between subspecies of other birds [0.0048 ± 0.0049 (Barrowclough 1980)], but it is only slightly below the range given by Barrowclough, 0.0078–0.1267, for congeneric species. The $\bar{D}$ between noncongeneric species in the Odontophorinae, 0.412, is considerably less than the $\bar{D}$ between these and the other phasianids, 1.32. Both of these values are greater

TABLE 2. Mean genetic distance (Nei 1978) as a function of taxonomic rank in some galliform birds. Taxa included in each taxonomic level are given in Appendix 1. $\bar{D}$-values from Table 1. Also given are $\bar{D}$-values at comparable taxonomic levels for other birds (from Barrowclough 1980).

Taxonomic level	Number of comparisons	$\bar{D}$ ± SD	Range	Comparable data for other birds
Local population	6	0.0007 ± 0.0013	−0.00151 to 0.00331	0.0024 ± 0.0028
Congeneric species (*Lophortyx*)	3	0.0067 ± 0.0014	0.00507 to 0.00775	0.0440 ± 0.0220
Noncongeneric species in Odontophorinae	46	0.4116 ± 0.2021	0.0824 to 0.7460	0.2136 ± 0.1659
Species in Odontophorinae vs. *Phasianus colchicus*, *Coturnix coturnix*, and *Alectoris chukar*	62	1.3210 ± 0.1640	0.962 to 1.654	not available
Tympanuchus pallidicinctus (Tetraonidae) vs. all other species (Phasianidae)	16	1.4000 ± 0.1500	1.041 to 1.668	0.6829[a] ± 0.1970

[a] Based on study by Barrowclough et al. (1981) of some procellariiform birds.

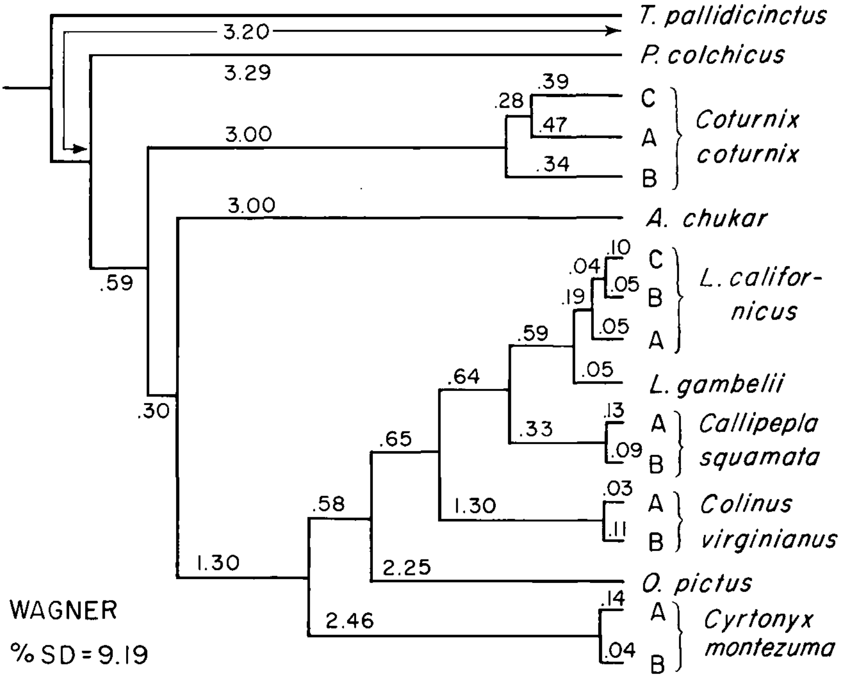

Fig. 2. Wagner tree based on Rogers' D-values. Branch lengths in units of Rogers' D (×10). The tree is "rooted" at *T. pallidicinctus* (Farris 1972).

than that given by Barrowclough (1980) for other avian confamilial but noncongeneric comparisons ($\bar{D} = 0.2136$), suggesting that the Odontophorinae is a distinct group. At the family level, the $\bar{D}$ observed between *T. pallidicinctus* (Tetraonidae) and the other species (all in Phasianidae), 1.400, is approximately twice the $\bar{D}$ reported for interfamilial comparisons of other birds (0.6829).

Genic relationships among species.—For two reasons, phenetic (UPGMA and WPGMA) and cladistic (Wagner and F-M) procedures were used to construct branching diagrams (Figs. 1–3). First, we wanted to determine whether or not the branching structure was dependent on which methods were used (see Presch 1979). Second, the methods for constructing trees, as opposed to phenograms, are independent of the assumption of homogeneity of evolutionary rates and, hence, provide estimates of the amount of genic change along branches; Felsenstein (1978) discusses these assumptions for Wagner trees.

The UPGMA and WPGMA phenograms had equal r_{cc}'s (0.99) and were topologically similar; therefore, only the UPGMA phenogram is shown (Fig. 1). The Wagner (Fig. 2) and F-M (Fig. 3) trees resemble Fig. 1 in terms of the overall relationships suggested. Differences among these three analyses suggest to us that the branching sequence of the subfamilies, while themselves genically distinct in all analyses, is unresolved by this analysis. That is, we do not believe that a clear hypothesis of the branching order of the subfamilies emerges from our data. The level of differentiation and the branching diagrams show considerable divergence, at the structural gene level, among these galliform birds. The branching sequence of taxa within the Odontophorinae was identical in all branching diagrams; therefore, we feel that it is a robust result.

The branching diagrams show that there is considerable divergence among taxa within the Ondontophorinae, and we now discuss relationships in that group. Given the patterns in Figs. 1–3, it seems unlikely that the level of divergence among local populations would be sufficient to alter among-species patterns established here. Thus, we doubt that an analysis of geographic variation, not addressed here, would alter our conclusions, which follow. *Lo-*

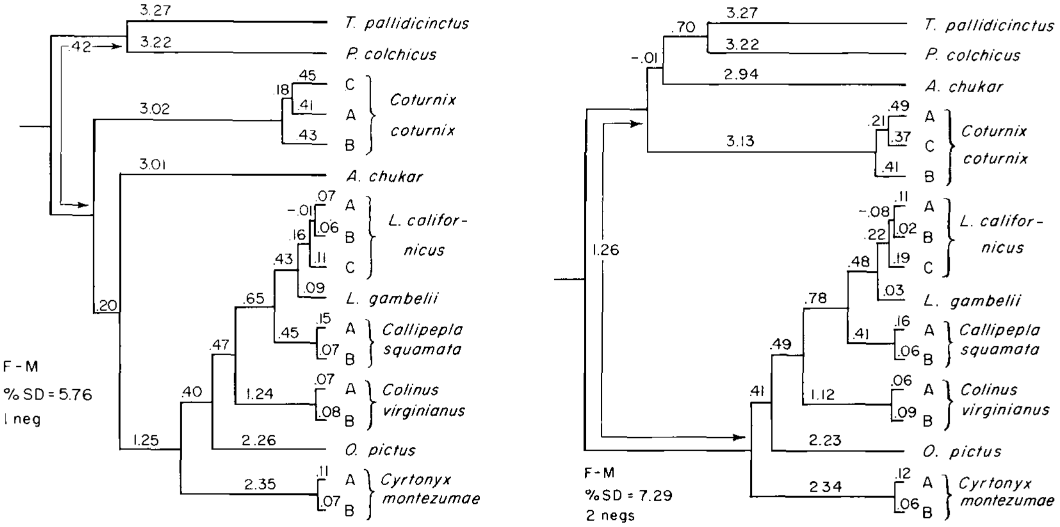

Fig. 3. Fitch-Margoliash (F-M) trees based on Rogers' D-values. Branch lengths in Rogers' D (×10). These two trees, of four examined, best summarized the original matrix, as judged by the values of the percentage of standard deviation and the number of negative branches. These trees, as well as those in Figs. 1 and 2, show that alternative hypotheses exist regarding the branching sequence of the five subfamilies.

phortyx gambelii and *L. californicus,* the only congeners in our study, consistently cluster together—the only genetic differences we found between them are minor gene frequency differences (Appendix 2). *Lophortyx* and *Callipepla* are the most similar pair of genera in our sample of Odontophorinae. The other genera in the subfamily, *Colinus, Oreortyx,* and *Cyrtonyx,* are each genically distinct, as evidenced by the level of separation on phenograms and branch lengths on F-M and Wagner trees. At αGpd-1, all members of the Odontophorinae are fixed for the same, apparently derived allele. Various groups of taxa in the subfamily are fixed for alleles not found in any non-Odontophorine taxon at Udh, Pept-1, Pept-2, and Est-2. The relationships among *P. colchicus, C. coturnix, C. virginianus, L. gambelii,* and *L. californicus* are similar to those suggested by Jolles et al. (1979) based on lysozyme sequence data.

DISCUSSION

Levels of genetic differentiation.—It is fairly well established that genetic differentiation among passerine taxa is low relative to other vertebrates (Avise et al. 1980c, Barrowclough et al. 1981). The reasons for this are unclear (see Sibley and Ahlquist 1982, Avise et al. 1980c). We believe that the most reasonable comparisons involve congeneric, interspecific levels of differentiation, when comparing *across* vertebrate classes (Zink 1982). Avian species limits are usually clearly defined, whereas higher taxonomic categories are far more arbitrary, especially across vertebrate classes. Thus, it is important to note that passerine congeners show little genic differentiation. Research should address this problem rather than differences between intergeneric or familial levels of genic divergence across vertebrate classes. Unfortunately, our only congeneric comparison, *L. gambelii-L. californicus,* is between probable sibling species.

Within a major vertebrate classes, comparisons of equivalent taxonomic levels above the species level may be more appropriate. The demonstration (Barrowclough and Corbin 1978, Barrowclough et al. 1981, Zink 1982, this study) that avian genetic distances increase as the taxonomic unit compared is more inclusive suggests that the taxonomic hierarchy reflects biological, or phylogenetic, units. We found that, at the generic and family levels, the galliforms are considerably more differentiated than passerine taxa (Table 2). We clearly require more comparisons of nonpasserine taxa before we will understand whether or not nonpasserines present a different pattern from that of passerines. For example, the genetic distances we observed may be among the highest found in nonpasserines, but this remains to be documented.

Rates and dates of divergence.—The branch lengths of the Wagner (Fig. 2) and F-M (Fig. 3) trees can be interpreted as rough estimates of "rates" of genic divergence, thereby indicating lineages that have changed faster or slower relative to other lineages. Rates are averages across loci. The branch lengths (rates) in Figs. 2 and 3 appear homogeneous, although with missing extant taxa this is difficult to judge, because additional taxa might have evolved at different rates than the taxa we sampled. The branch lengths (Fig. 2) from the "most recent common ancestor" to members of the Odontophorinae range from 2.29 (to *C. squamata*) to 2.83 (to *O. pictus*), and the mean (±SD) equals 2.59 ± 0.17; thus, we suggest that evidence of rate heterogeneity is lacking among these taxa.

Nei's measure of genetic distance can be converted into approximate dates of divergence between taxa (Nei 1975). Nei suggested a "theoretical" conversion of $t = 5 \times 10^6 D$, where t is time since divergence from a common ancestor, and D is Nei's D-value. Yang and Patton (1981) used this conversion to estimate divergence dates among Galapagos finches. As Yang and Patton and Avise et al. (1980c) noted, other attempts to calibrate D-values (e.g. Sarich 1977) suggest that Nei's calibration may be low (i.e. too rapid) by a factor of four. Workers with other vertebrate groups (e.g. Maxson and Maxson 1979) have used the fossil record and independent estimates from microcomplement fixation studies to calibrate electrophoretic distances and divergence times, and such studies have tended to support Sarich (1977).

The fossil record of the galliforms allows what amounts to the first independent calibration of avian genetic distances. Several assumptions are made in our calibration. First, based on our reading of Holman's (1961, 1964) extensive osteological analyses, we assume that the Odontophorinae is a monophyletic group consisting of two subgroups: the *Odontophorus* group (consisting of *Odontophorus*, *Dactylortyx*, *Cyrtonyx*, and *Rhynchortyx*) and the *Dendrortyx* group (containing *Dendrortyx*, *Philortyx*, *Oreortyx*, *Colinus*, *Callipepla*, and *Lophortyx*). Derived character states (synapomorphies) support the monophyly of the Odontophorinae and each of the two subgroups.

Of interest here is *Cyrtonyx cooki*, an extinct species from the mid-Miocene [16 million yr before present (MYBP)] of Nebraska (Brodkorb 1964) and a congener of a species examined by us (*C. montezumae*). We assume here that this fossil belongs to the monophyletic lineage *Cyrtonyx*, and it is neither from the Odontophorine stock that pre-dated the *Dendrortyx*-*Odontophorus* split, nor is it a primitive (pleisomorph) early member of the *Dendrortyx* group. Thus, the age of *C. cooki* can be taken as a conservative estimate of the age of the *Cyrtonyx* lineage, represented in our study by *C. montezumae*. The average of D-values from *C. montezumae* to its sister taxa in the Odontophorinae (Fig. 1, Table 1), 0.609, is assumed to represent minimally 16 million yr (MY). This results in the following conversion: $t = 26.3 \times 10^6 D$. We use this calibration to indicate possible dates of divergence among the taxa shown in Fig. 1. We stress that this is a rough estimate (but probably conservative), owing to the variance of genetic distances between taxa. It is the first such approximation for an avian taxon.

Holman (1961) discussed a fossil, *Lophortyx shotwelli*, from Umatilla County, Oregon. This specimen is associated with mammalian remains from the Hemphillian stage, dated at 6 MYBP (Savage pers. comm.). Holman noted that this specimen possessed several characters unlike modern *Lophortyx*, and therefore its position in the evolutionary history of *Callipepla* and *Lophortyx* is uncertain. If this fossil is a "good" member of either *Callipepla* or *Lophortyx*, it would greatly alter our calibration of genetic distances. For instance, our estimated date of the divergence of *Callipepla* and *Lophortyx*, 2.8 MYBP, would necessarily be ≥6 MYBP, or twice our present estimate. Prager et al. (1974) suggested that phasianoid transferrins evolved at a rate of 0.97/MY. Prager and Wilson (1976) gave a transferrin immunological distance of 65 for *P. colchicus*-*C. virginianus*, or a divergence date of 63 MYBP. Our data ($D = 1.34$) suggest a divergence date of 35 MYBP. Unfortunately, this is the only comparison in common between our study and Prager and Wilson's (1976). It is of interest that their estimate of the divergence date for these two taxa is twice ours and in the same direction as our estimate would be if *L. shotwelli* was a valid *Lophortyx*. Clearly,

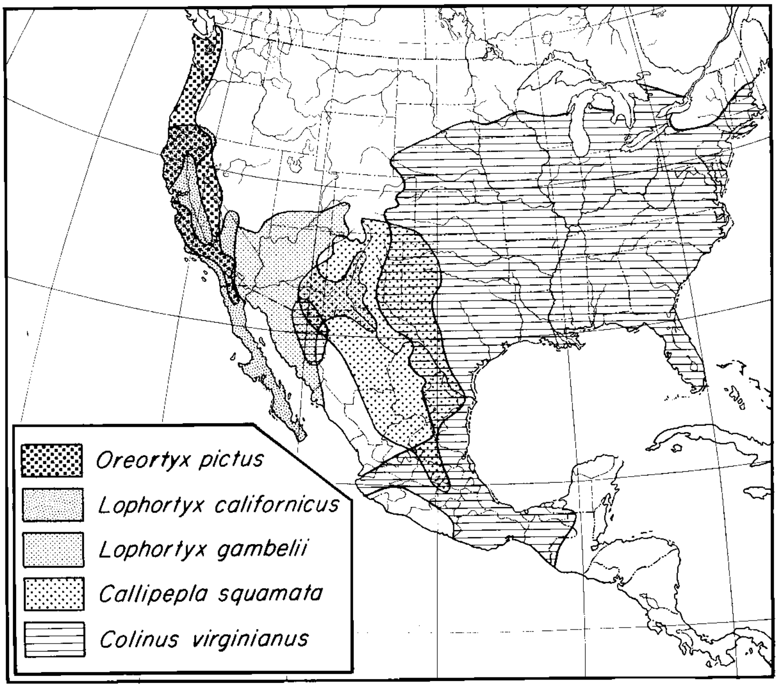

Fig. 4. Approximate breeding distributions (excluding introductions) of *Oreortyx pictus, Colinus virginianus, Callipepla squamata, Lophortyx gambelii,* and *L. californicus.* These species are all representatives of the subfamily Odontophorinae. Ranges taken from Leopold et al. (1981).

the discrepancy in our estimates deserves future attention, as does the phylogenetic position of *L. shotwelli.* We conclude at this time that Nei's (1975) conversion factor given above is probably low by a factor of five for the galliforms studied here. We note also that many assumptions, such as phylogenetic hypotheses of fossil and recent forms, need to be tested.

Biogeography of the Dendrortyx *group of the Odontophorinae.*—As mentioned above, the *Dendrortyx* group of the Odontophorinae consists of the genera *Dendrortyx, Philortyx, Oreortyx, Colinus, Callipepla,* and *Lophortyx.* Although we lack *Dendrortyx* and *Philortyx* in our genetic analysis, we will use the phylogeny of the remaining taxa and our approximate dating of cladogenetic events (Fig. 1) to develop an evolutionary perspective of the biogeography of these taxa. Without an objective estimate of phylogenetic relationships, it would be difficult to evaluate historical evolutionary patterns among these New World quail given simply a map of their current distributions (Fig. 4).

The earliest known fossil Odontophorinae are from the early Oligocene of Saskatchewan, the middle Oligocene of Colorado, and the lower Miocene (approximately 20 MYBP) of South Dakota (Brodkorb 1964). This suggests a fairly widespread distribution of ancestral Odontophorine stock. Therefore we will apply methods from vicariance biogeography (Nelson and Platnick 1981) to generate our biogeographic hypothesis. We assume first that the *Dendrortyx* and *Odontophorus* groups are distinct, monophyletic lineages (discussed above) that diverged at least 16 MYBP (middle Miocene). Next, we assume that *Dendrortyx* and *Philortyx* are primitive and/or have not affected the distribution of the remaining species. The restricted distribution of *Dendrortyx* (México to Costa Rica) and *Philortyx* (México) suggests relict status and, therefore, "primitiveness." Based on their skeletal morphology, Holman (1961) concluded that these two genera were the most primitive members of the *Dendrortyx* group. These assumptions obviously need testing.

The remaining steps in our biogeographic hypothesis are outlined *diagrammatically* in Fig. 5. The genetic data indicate that *O. pictus* originated about 12.6 MYBP (Fig. 5a) and probably evolved in western North America, based on its current distribution (Fig. 4). Perhaps drying trends at this time (Axelrod 1979) resulted in the invasion of more mesic environments of higher elevation by *Oreortyx*. The southward displacement of land west of the San Andreas Fault at this time might also have isolated this taxon (see Wenner and Johnson 1980). Another east-west split of an ancestral taxon resulted in the divergence of *Colinus* (Fig. 5b), estimated by our data at 7.0 MYBP. The earliest known fossils of *Colinus* (Holman 1961, Brodkorb 1964) are from the upper Pliocene of Kansas. Because our estimated divergence date is well before upper Pliocene, the sites of fossil *Colinus* do not permit identification of the area of origin of *Colinus*.

Penultimately, *Callipepla* and *Lophortyx* diverged (Fig. 5c), about 2.8 MYBP, or late Pliocene, when their ancestor was fragmented in the southwestern aridlands of North America. Axelrod (1979) noted that during the late Pliocene isolated arid and semi-arid desert patches existed in the current Sonoran and Chihuahuan desert regions, and this could have allowed the allopatric differentiation of *Callipepla*, which presently occupies such habitats (Leopold et al. 1981). Species of *Lophortyx* diverged last, resulting in the current distribution patterns (Fig. 4). It will be of value to ascertain the phylogenetic position of *L. douglasii*.

Hubbard (1973) proposed a vicariant biogeographic explanation for the evolution of species in the genera *Lophortyx* and *Callipepla* (consid-

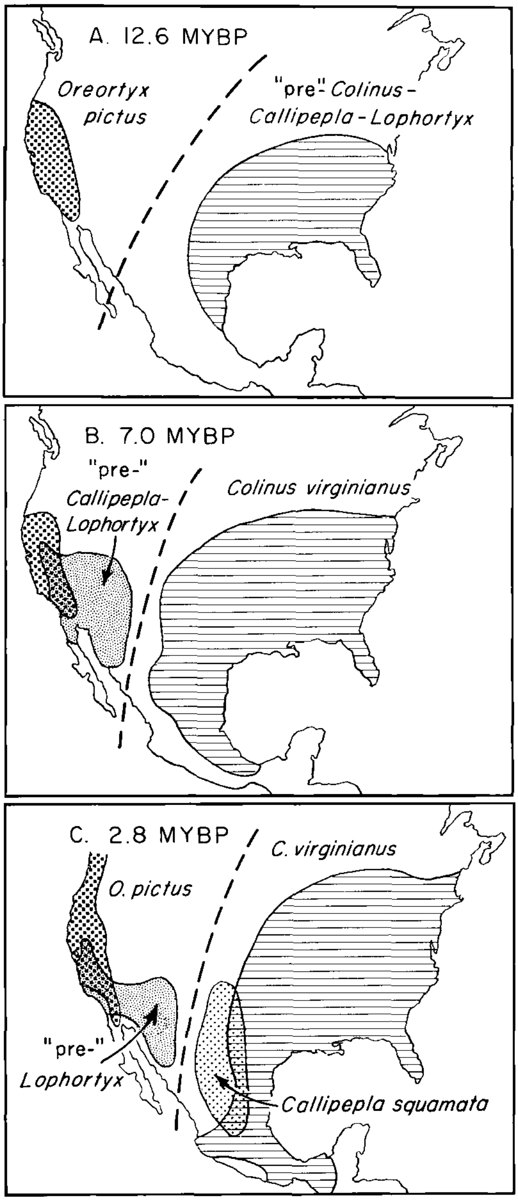

Fig. 5. Diagrammatic representation of hypothetical stages in the evolution of species shown in Fig. 4. Because historical ranges are unknown, ranges should not be interpreted strictly. The primary information we wish to convey is the isolation events, which are indicated by the dashed lines. The exact position of the dashed lines is speculative, however. Therefore, whether differentiation among these taxa was parapatric or allopatric and the extent of any gaps between taxa during their evolution are unknown. After each isolation event, dispersal probably occurred across these boundaries. A. Separation of *Oreortyx pictus*, 12.6 MYBP, presumably in areas consisting of evergreen chaparral, evergreen-broadleaf forest, or coniferous forest with shrub understory in western North America. B. Origin of *Colinus virginianus*, 7.0 MYBP. Present habitat is essentially weedy fields bordered by brush or woodlots, although in tropical lowlands it occurs in wetter conditions. The exact location of the origin of *C. virginianus* is uncertain. Note that the range of "pre" *Callipepla-Lophortyx* could have extended further east if *C. virginianus* was either isolated to the south or north. C. Divergence of *Callipepla squamata* and *Lophortyx*, 2.8 MYBP, probably concurrent with late Pliocene disjunct patches of arid and semi-arid desert. *C. squamata* and *L. gambelii* are typically found in desert scrub or arid grasslands, while *L. californicus* occurs in oak woodland, chaparral, and brushy foothills.

ered by him congeneric), which involved hypothetical ancestors and their distributions and Pleistocene glaciation cycles. According to Hubbard's scenario, a trichotomous split produced *C. squamata*, *L. douglasii*, and "*pre-californicus-gambelii*" in the Illinoian glacial epoch, with *L. californicus* and *L. gambelii* differentiating in the Wisconsinian glacial period. Using the genetic distance conversion established above, we estimate the split of *L. gambelii* and *L. californicus* at 190,000 yr ago, and that of *Lophortyx* and *Callipepla* at 2.8 MYBP, or roughly late Pliocene. While Hubbard is correct in assuming that a minimum of two geologic events (e.g. glacial-interglacial cycles) is needed to account for the distribution patterns of extant *Callipepla* and *Lophortyx*, these genera probably diverged well before the times he suggested. Illinoian age glacial cycles may well have effected speciation in *Lophortyx*, however.

This biogeographic reconstruction is a hypothesis. We note that sympatry of breeding species, which is considerable among the species studied here (Fig. 4), implies dispersal (Nelson and Platnick 1981). Thus, it is difficult to determine the relative importance of vicariance or dispersal in accounting for the evolutionary patterns in this group. Also, geological and paleobotanical evidence is sufficiently fragmentary (see Axelrod 1979, Wenner and Johnson 1980) to prevent precise correlations with our phylogenetic hypothesis. That is, we lack a well corroborated "area cladogram" (Nelson and Platnick 1981).

Our phylogenetic hypothesis and dating of cladogenetic events suggest that a series of three east–west range disjunctions (Fig. 5) could explain the evolution of these genera of New World quail. These patterns need to be corroborated with studies of other avian groups, as well as other groups of vertebrates and nonvertebrates. We believe, however, that our hypothesis (Fig. 5) is an important first approximation of the evolutionary history of these quail taxa and makes objective, testable predictions that would otherwise be difficult given only the map of current breeding distributions. We also wish to demonstrate that molecular methods of inferring phylogenies can be combined with information from the fossil record to further understanding of evolutionary patterns in avian groups.

Taxonomy.—Mayr and Short (1970) suggested that *L. gambelii* and *L. californicus* are conspecific. The genetic data presented here are consistent with this idea. Wild hybrids (Henshaw 1885, Miller and Stebbins 1964) between the forms include only the F_1 generation, however, which suggests a lack of introgression and panmixia in zones of sympatry. Furthermore, hybrids have been reported for other sympatrix quail [e.g. *Colinus virginianus* × *L. californicus* (Aiken 1930); *Callipepla squamata* × *L. gambelii* (Bailey 1928); *L. californicus* × *C. squamata* (Jewett et al. 1953); *C. virginianus* × *C. squamata* (Johnsgard 1973); *O. pictus* × *L. californicus* (Peck 1911)]. Incidence of hybridization is probably not an accurate predictor of close phylogenetic relationship, because birds retain the ability to hybridize despite considerable genetic divergence (Prager and Wilson 1975). The apparent lack of prereproductive isolating barriers in sympatry, at least to F_1 hybridization, does not necessarily indicate recency of common ancestry or close phylogenetic relationships among these quail. Therefore, we reject the notion that hybrids between *L. gambelii* and *L. californicus* prove conspecific status. As only the F_1 hybrids and not a hybrid swarm have been found, these are probably distinct biological species. We also point out that the evidence supporting apparent assortative mating in sympatry overshadows our finding a *D*-value typical of subspecies between these taxa. Clearly distinct species can be genically similar (Avise et al. 1980b, c).

Several authors (e.g. Mayr and Short 1970, Johnsgard 1973, and references therein) have suggested merging *Lophortyx* and *Callipepla*. These genera are clearly similar (Fig. 1). The $\bar{D}$ between our samples of these two taxa, 0.104, is one-half that reported by Barrowclough (1980) for similar avian intergeneric comparisons; yet it is within the range (0.0126–1.214). Thus, our data provide no clear-cut answers, and we suggest that the decision regarding their taxonomic status be made on the basis of other kinds of biological evidence.

The suggestion by Phillips et al. (1964) and Mayr and Short (1970) that *Oreortyx* be merged with *Callipepla* (including *Lophortyx*) is not consistent with our molecular data (Figs. 1–3). It would also require inclusion of *Colinus*; otherwise, the new taxon would not be monophyletic. We think that merging these taxa would obscure their relatively long, independent, evolutionary histories. We recognize, however, that there can be no absolute value of genetic distance on which to base taxonomic decisions. The external phenotypic resemblance of Mountain and California quail does not, in this case, indicate a close phylogenetic relationship. Furthermore, Hudson et al. (1959, 1966) and Holman (1961) provide data on the myology and skeletal morphology, respectively, that show that *Oreortyx* is morphologically distinct from other members of the *Dendrortyx* group. Gutiérrez (1980) reported that *Oreortyx* was very different ecologically from *Lophortyx*. Thus, genetic, morphologic, and ecologic data show that *Oreortyx* is not a close relative of *Lophortyx* or *Callipepla*, and there seems to be no basis for their generic merger.

The systematic status of *C. virginianus* is uncertain. It is shown here to be a distinct clade within the Odontophorinae and more similar to *Lophortyx* and *Callipepla* than to *Oreortyx* and *Cyrtonyx*.

Some authors (Brodkorb 1964, Mayr and Short 1970, Johnsgard 1973) consider the Tetraonidae a subfamily of the Phasianidae. Our data (Table 1) show that the distance from *T. pallidicinctus* (Tetraonidae) and *P. colchicus* (Phasianidae) to all other species is similar. Thus, it might be appropriate to consider such a taxonomic scheme.

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APPENDIX 1. Location, sample sizes, and sample collection dates. Different populations of the same taxon are labeled by upper case letters, which correspond to the letters used in Appendix 2, Table 1, and the figures. The taxonomic framework is from Peters (1934).

Taxon	Number of individuals	Locality and date
Tetraonidae		
Lesser Prairie Chicken (*Tympanuchus pallidicinctus*)	13	New Mexico: 8 mi E Milnesand, Roosevelt Co., December 1975.
Phasianidae		
Phasianinae		
Ring-necked Pheasant (*Phasianus colchicus*)	13	California: Webb Tract, Sacramento Delta, Sacramento Co., November 1975.
Perdicinae		
Common Quail (*Coturnix coturnix*)	30	Avian Sciences Department, University of California, Davis, California, A—Big Brown Strain (n = 10). B—Small Brown Strain (n = 10). C—Albino Strain (n = 10). A, B, and C obtained in February 1976.
Chukar (*Alectoris chukar*)	12	Avian Sci. Dept., Univ. Calif., Davis. (n = 10), February 1976; 5 mi SE Panoche, San Benito Co., California (n = 2), Jan. 1976; samples combined.
Odontophorinae		
Dendrortyx Group		
California Quail (*Lophortyx californicus*)	36	California: A—5 mi E Shandon, San Luis Obispo Co. (n = 6), December 1974. B—5 mi N Jolon, Monterey Co. (n = 13), December 1974. C—4 mi E Mercy Hot Springs, Fresno Co. (n = 9), October 1975 and (n = 2) in January 1976; 5 mi SE Panoche, San Benito Co. (n = 6), January 1976.
Gambel's Quail (*L. gambelii*)	22	New Mexico: 1 mi E Columbus, Luna Co. (n = 19), December 1975. Arizona: 10 mi E Green Valley, Pima Co. (n = 3), January 1976; samples combined.
Scaled Quail (*Callipepla squamata*)	29	New Mexico: A—8 mi E Milnesand, Roosevelt Co. (n = 7), December 1975. B—1 mi E Columbus, Luna Co. (n = 20), December 1975. Arizona: 10 mi E Green Valley, Pima Co. (n = 2), January 1976; combined with population B as there was no differentiation.
Bobwhite Quail (*Colinus virginianus*)	15	New Mexico: A—8 mi E Milnesand, Roosevelt Co. (n = 8), December 1975. B—18 mi NE Milnesand, Roosevelt Co. (n = 7), December 1975.
Mountain Quail (*Oreortyx pictus*)	16	California: 2 mi SE Jamesburg, Monterey Co. (n = 16), June–August 1975.
Odontophorus Group		
Montezuma Quail (*Cyrtonyx montezumae*)	31	Arizona: A—15 mi E Patagonia, Santa Cruz Co. (n = 23), January 1976; B—10 mi W Patagonia, Santa Cruz Co. (n = 8), January 1976.

APPENDIX 2. Allelic frequencies for 23 presumptive loci in 10 species of gallinaceous birds. Numbers in parentheses are frequencies of alleles at a locus. A single letter denotes sample fixed for that allele. Full names for loci given in Yang and Patton (1981) or below. Names of taxa and sample sizes given in Table 1.

Locus	*T.p.*	*P.c.*	*C.c.* A	*C.c.* B	*C.c.* C	*A.c.*	*L.g.*	*L.c.* A
PGI	b	c	d (0.65) e (0.35)	d (0.60) e (0.40)	e	c	b	b
ADA[a]	g	b	d (0.35) f (0.65)	f	f	e	a (0.42) c (0.58)	a (0.06) c (0.94)
PGM-1	a	c	d	d	d	d	b	b
MPI	h	c	f	e (0.60) f (0.40)	f	a	e	e (0.94) g (0.06)
IDH-1	e	d	c	c	c	d	a (0.97) f (0.03)	a
IDH-2	g	b	g	g	g	a (0.30) c (0.70)	f	f
αGPD-1	d	c	e	e	e	a	b	b
αGPD-2	c	c	d	d	d	a	b	b
ME[b]	g	d (0.12) e (0.88)	a (0.25) b (0.75)	a (0.45) b (0.55)	a (0.40) b (0.60)	f	f	e (0.03) f (0.97)
GOT-1	i	j	h	h	h	a (0.45) b (0.05) c (0.50)	g (0.97) i (0.03)	g
GOT-2	a	b	b	b	b	a	b	b
GDH[c]	a	c	b	b	b	b	b	b
UDH[d]	d	d	d	d	d	d	c	c
SDH	a	e	a	a	a	b (0.15) c (0.85)	d	d
LDH-1	a	a	c	c	c	b	b	b
LDH-2	a	a	c	c	c	b	b	b
Pept-1	g	a	b	b	b	a	c	c
Pept-2	d	d	e	e	e	a	b	b
Alb	g	c	d (0.95) f (0.05)	c (0.40) f (0.60)	c	b	e	c (0.12) e (0.88)
Est-1	a	c (0.08) d (0.92)	e	d (0.60) e (0.40)	e	f	f (0.05) g (0.95)	f (0.03) g (0.97)
Est-2	g	g (0.38) h (0.62)	f	f	f	e	b	a (0.03) b (0.97)
6PGD	d	g	f (0.85) h (0.15)	e (0.05) f (0.80) h (0.15)	f (0.75) h (0.25)	c (0.10) d (0.90)	d	b (0.03) d (0.97)
XDH[e]	g	f	a (0.30) c (0.70)	b (0.05) c (0.95)	a (0.20) c (0.80)	c	a (0.08) c (0.92)	a (0.03) c (0.97)
Percentage polymorphism	0.0	11.1	22.2	25.9	11.1	14.8	18.5	29.6
Heterozygosity	0.0	2.6	4.8	8.9	4.8	5.2	2.5	2.8
Mean number alleles per polymorphic locus	—	2.0	2.0	2.1	2.0	2.2	2.0	2.0

[a] Adenosene de-aminase.

[b] Malic enzyme (NADP dependent).

[c] Glutamate dehydrogenase.

[d] Unidentified dehydrogenase.

[e] Xanthine dehydrogenase.

APPENDIX 2. Continued

L.c. B	*L.c.* C	*C.s.* A	*C.s.* B	*C.v.* A	*C.v.* B	*O.p.*	*C.m.* A	*C.m.* B
b	b	b	b	b	b	a	b	b
c	c	a	a (0.75) c (0.25)	a (0.56) c (0.44)	a (0.50) c (0.50)	e (0.97) g (0.03)	c	c
b	b (0.96) d (0.04)	c	c	c	c	b	c	c
e (0.83) g (0.17)	e (0.92) c (0.04) g (0.04)	e	e (0.75) g (0.25)	d	d	b	g (0.91) i (0.09)	g (0.94) i (0.06)
a	a	a	a	a	a (0.93) c (0.07)	a	b	b
f	c (0.11) f (0.89)	f	f	f	f	f	d (0.04) e (0.96)	e (0.94) g (0.06)
b	b	b	b	b	b	b	b	b
b	b	b	b	b	b	b	b (0.85) d (0.15)	b (0.87) d (0.13)
f	f	f	f	b (0.06) e (0.94)	e	c	e	e
g	g (0.92) i (0.08)	g (0.71) j (0.29)	f (0.05) g (0.70) j (0.25)	d (0.06) g (0.94)	g	g	g	e (0.13) g (0.87)
b	b	b	b	b	b	b	b	b
b	b	b	b	b	b	b	b	b
c	c	c	c	c	c	b	a	a
d	d	d	d	d	d	b (0.63) d (0.37)	b	b
b	b	b	b	b	b	b	b	b
b	b	b	b	b	b	b	b	b
c	c	c	c (0.97) f (0.03)	d	d	c (0.06) f (0.94)	e	e
b	b	b	b	b	b	b	c	c
c (0.08) e (0.92)	c (0.15) e (0.85)	e	e	a	a	e	a	a
g	g	g	g	h	h	f	a (0.83) b (0.15) c (0.02)	a (0.87) b (0.13)
b	b	b	b	b	b	s	c	b (0.19) c (0.81)
d	d	d	d	d	b (0.07) d (0.93)	d	d (0.96) f (0.04)	d
c	c	a (0.07) d (0.93)	a (0.10) d (0.90)	a (0.94) e (0.06)	a (0.86) e (0.14)	f	e	e
7.4	18.5	7.4	18.5	14.8	14.8	11.1	18.5	22.2
1.8	3.4	1.6	3.7	2.8	2.6	2.1	2.4	5.1
2.0	2.2	2.0	2.2	2.0	2.0	2.0	2.2	2.0

NEST ATTENDANCE OF PARENT BIRDS IN THE PAINTED SNIPE (*ROSTRATULA BENGHALENSIS*)

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ABSTRACT.—I observed 15 pairs of Painted Snipes (*Rostratula benghalensis*) in Japan for 24-h periods in order to compare the nest attendance behavior of males and females and to document changes in their behavior during the laying period. From a few days before the laying of the first egg until the day the second egg was laid, the male and female consorted with each other (stayed within 5 m of each other) more than 90% of the observation time. They visited the nest repeatedly on the first and second days of laying. On the third day, the consorting ratio decreased to 58.5%, and the male typically started to incubate. He continued to incubate that night. After laying the third egg, the female usually did not visit the nest except to lay the fourth and last egg. The male continued incubation, and the female met her mate only when she laid the last egg. The absence of female incubation and the early termination of consorting behavior are consistent with the possibility that Painted Snipe females are polyandrous. *Received 12 January 1982, accepted 4 October 1982.*

AMONG the polyandrous charadriiform species, comprehensive studies of pair-bond maintenance have been conducted on only four species, the Northern Jacana (*Jacana spinosa*; Jenni and Collier 1972, Jenni and Betts 1978), the Spotted Sandpiper (*Actitis macularia*; Hays 1972, Oring and Knudson 1972, Maxson and Oring 1980), the Red-necked Phalarope (*Phalaropus lobatus*; Hildén and Vuolanto 1972), and the Red Phalarope (*Phalaropus fulicaria*; Schamel and Tracy 1977). Although a detailed study of the Painted Snipe (*Rostratula benghalensis*) has not been conducted, sex role reversal and an apparently unbalanced sex ratio suggest the possibility of polyandry in this species (Beven 1913, Baker 1935, Lack 1968, Hays 1972, Oring and Knudson 1972, Jenni 1974). The objectives of this study were (1) to compare the nest attendance of male and female Painted Snipes, (2) to measure the amount of time the members of the pair spend together (consorting ratio) during laying and incubation periods, and (3) to consider the evidence for polyandry.

STUDY AREAS AND METHODS

Field observations were made in two areas. The preliminary study was done in Chuzu Town, southeast of Lake Biwa, central Japan (136°02′E, 35°08′N), from May to June 1978 (Biwa area). Nest observations were conducted in 20-ha abandoned fields among paddy fields at an elevation of about 85 m. Marshy plants, mainly buttercup (*Ranunculus quelpaertensis*), bitter cress (*Cardamine lyrata*), foxtail (*Alopecurus aequalis*), and cudweed (*Gnaphalium affine*), grew sparsely in these abandoned fields. The water depth in this area varied from 0 to 15 cm.

The main study was conducted in Toyo City, northwestern Shikoku Island, Japan (133°03′E, 33°57′N), from March to August 1979 (excluding May) and from June to July 1980 (Toyo area). This 40-ha study area of reclaimed land faces the Japanese Inland Sea. A quarter of the area was used as paddy fields, and the rest was marshy grassland that was plowed once or twice a year, usually in June and July. The study area was traversed by six parallel roads 200 m apart and by another road that intersected them at right angles. This poorly drained area was always covered with water. Until it was plowed, dense reed (*Phragmites communis*) or bulrush (*Scirpus planiculmis*) grew there every year. After it was plowed, the grasses grew only patchily or sparsely before September. The Toyo area is about 300 km west of the Biwa area.

Most data for the field study were obtained by continuous observations. Observations that started after 1800 are identified as "nocturnal observations" and were made with the aid of a flashlight. Behavior was observed with binoculars (9×) and a spotting scope (15×). Behavioral acts were recorded in seconds, and the data were later converted to minutes for calculations. Of 27 birds observed, 4 males and 2 females were marked with neck bands. Because no other birds of the same sexes as the banded individuals were observed entering their nests, any male or female who entered a nest was considered the progenitor of the eggs in the nest.

All observations reported here were made at nests with four eggs. The four eggs were laid on consecutive days, and the days of laying were identified as

TABLE 1. The length of visits to the nest during the laying period (minutes ± SD). Numbers in parentheses indicate nocturnal visits.

	Day 1	Day 2	Day 3	Day 4
Female				
Length of egg-laying visits	35.5 ± 17.5	62.3 ± 33.4	32.8 ± 7.4	15.9 ± 1.9
Number of egg-laying visits	2	4	5	6
Length of other visits	3.6 ± 3.7	6.1 ± 5.2	5.7 ± 5.3	1 —
Number of other visits	43	50	36	1
Male				
Length of visits	3.6 ± 8.0	8.0 ± 12.8	22.6 ± 31.7 (21.6 ± 15.1)	43.4 ± 52.8 (36.1 ± 10.2)
Percentage of stays longer than 30 min	2.0	6.8	26.2 (35.3)	46.8 (76.9)
Number of visits	99	85	92 (17)	47 (13)
Number of nests	4	7	9 (1)	8 (1)

day 1, day 2, and so on. These four days comprise the laying period. A span of a few days before day 1 is referred to as the prelaying period. The incubation period extends from the day after day 4 until hatching.

The percentage of time during which the two members of a pair stayed within 5 m of each other was termed the consorting ratio. Consorting behavior was studied at the Toyo area for a total of 17 days (162.0 h). Other observations were made at both the Toyo and Biwa areas.

Nest-related behavior in the Biwa area was observed from blinds about 10 m from the nests. Four nests were observed for a total of 17 days (190.8 h). Observations were made at the Biwa area during two nights (22.6 h) of the incubation period. All diurnal observations at the Toyo area were made from a blind on a car roof 1.5 m above the ground. By driving the car along the roads, I was able to follow the birds when they left their nests. Nine pairs were observed at the Toyo area for a total of 36 days (368.7 h) Two of these nine pairs abandoned their nests during the laying period, so the data from these nests were excluded from the results (total 7 days). Two nests were observed a total of four nights (47.0 h) during the laying period. Activity at night at the Toyo area was observed at intervals of 1 min from about 20 m when a flashlight was switched on for about 5 s and off for about 55 s.

RESULTS

Clutch size and time of laying.—Of 33 nests found, 2 had 3-egg clutches, 30 held 4 eggs, and only 1 held 5 eggs. Accordingly, the normal clutch size in this species is considered to be four.

The time of laying was recorded 17 times. During the laying period, a female laid an egg every morning between 0700 and 1100 (Fig. 1). She stayed on the nest far longer when coming to lay an egg than at other times (Table 1). The female was on the nest for a much shorter duration when she laid the fourth egg ($\bar{x}$ = 15.7 min) than when she laid the earlier eggs ($\bar{x}$ = 44.0 min). All other visits to the nest by the female during the laying period were much shorter ($\bar{x}$ = 5.1 min); 88.5% of these visits were less than 10 min.

On four additional days when the 1st, 2nd, or 3rd eggs were laid but egg laying was not observed, females stayed on the nest for 39, 42, 46, and 47 min between 0800 and 1210 (Fig. 1; 22 June 1979, 21 June 1978, 3 June 1978, and 12 June 1979, respectively). These four stays were the only long stay on those days. It is assumed that egg laying occurred during these long visits. Egg laying was not seen at two nests on day 4, but the females entered the nests only once, and it is assumed that they laid during these visits (Fig. 1; 30 March 1979 and 21 July 1979).

Nest visitation on each laying day.—On day 1, both sexes entered the nest frequently during the morning (Fig. 1), but they often left it for a long time during the afternoon. They returned to the nest in the evening. The male stayed about the same length of time (Table 1) and entered the nest about as frequently as the female did. No observations were made on the night of day 1.

On day 2, the duration of diurnal visits increased but the number of visits decreased

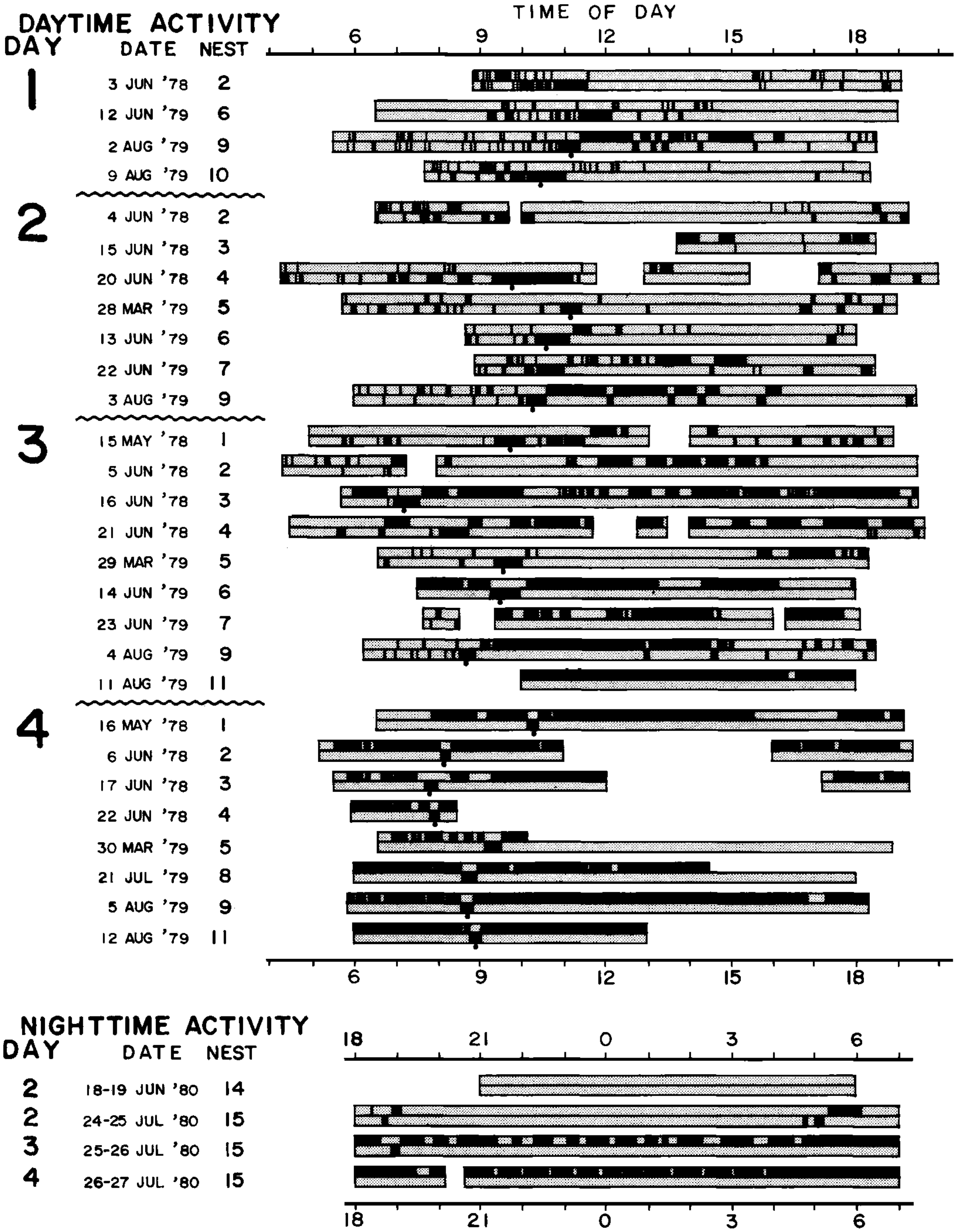

Fig. 1. Activity during laying period. Male is shown in upper and female in lower belt of each pair. Black band shows time spent on nest and shaded band out of nest. Small dot shows the time of egg laying. Day 1 is the first day of egg laying and day 4 the last day.

slightly in both sexes. In two nests watched at night, both sexes left the nest site just after dark and returned just before light. At Nest 15 the male and female left the nest at 1907 and returned at 0443. At Nest 14 the male and female were gone when observations started at 2100 and returned to the vicinity (within 5 m) of the nest at 0426.

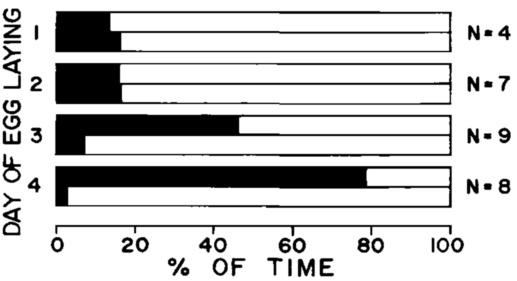

Fig. 2. Average percentage of daylight time on nest. Upper belt shows male stays and lower belt female stays. Black band shows percentage of time spent on nest and white band out of nest. Number of nests observed is shown.

TABLE 2. The percentage of daylight hours during which the male and female of a pair stayed within 5 m of each other.

	Average (range)	Number of hours observed	Number of pairs
Prelaying period	99.6 (98.5–100.0)	23.6	4
Laying period			
Day 1	99.0 (97.5–100.0)	34.0	3
Day 2	92.8 (89.3–95.9)	42.6	4
Day 3	58.8 (38.4–81.0)	29.7	3
Day 4	7.9 (3.3–16.7)	32.1	3

On day 3, both sexes changed their patterns of nest visitations, but in different ways. Females entered the nest repeatedly before laying the third egg but after that did not return to the nest until 1800 in all but two nests. Females entered three of four nests between 1800 and 1930. At Nest 15 the female entered the nest at 1851, left at 1903, and did not return that night, but her mate spent the night on the nest. During the day males visited the nest about as often as the previous day, but the average visit was much longer (Table 1).

On day 4, all but one of the females entered the nest only once and laid the last egg at that time. After leaving the nest, they were never seen near it again. At Nest 9 the female left the nest 1 min after entering it, but she returned 30 s later and laid the fourth egg. Males entered the nest less often than previously but stayed much longer during each visit. The males stayed on the nest at night, but females did not return to the nest.

Two males in the Toyo area abandoned their nests after their females laid the third egg, but the females still laid the fourth egg in the nests. Pair 12 visited their nest in typical fashion through day 3. On day 4, the female exhibited typical behavior. She entered the nest, laid the fourth egg, left the nest, and never returned. The male on day 4, however, never visited the nest, nor was he seen around the nest. I began observing Nest 13 on day 2. The male did not enter the nest between 0744 and 1157 on day 2, nor at any time on day 3, and he did not even visit the vicinity of the nest on day 4. His female stayed on the nest more than 40% of the total observation time on both days. On day 4 she stayed on the nest much longer than the other females. On her first visit she stayed for 27 min and laid the fourth egg. She then flew off and returned 80 min later and stayed on the nest for 5.5 h. Neither the male nor the female returned after day 4.

Total time spent on nest in laying period.—During the whole laying period of daylight hours, males stayed on the nest four times as much as females (39.8% vs. 9.9%). As egg laying advanced, males increased and females decreased the amount of time they spent on the nest (Fig. 2). On days 1 and 2, females spent slightly more time on the nest than males did (16.4% vs. 13.2% and 16.7% vs. 16.2%, respectively). On day 3 some males spent a longer time on the nest than previously, and it was on this day that the greatest range was seen in the percentages of time spent on the nest for different males. The males on five of the nine nests spent more than 50% of the day on the nest (46.2% on average, range 16.3%–71.3%). The females on day 3 reduced their time on the nest to only 7.3%. On day 4 the males spent 78.7% of the day on the nest, and females spent only 3.0%.

Females did not visit their nests at all at night during the laying period, and males did not visit at night until after the third egg was laid. A male spent 68.6% of the night following the laying of the third egg and 86.7% of the night following the laying of the fourth egg on the nest.

Male nest attendance in the Painted Snipe reached mid-incubation levels on day 3, and the incubation started on day 4. In the Red-necked Phalarope (Hildén and Vuolanto 1972),

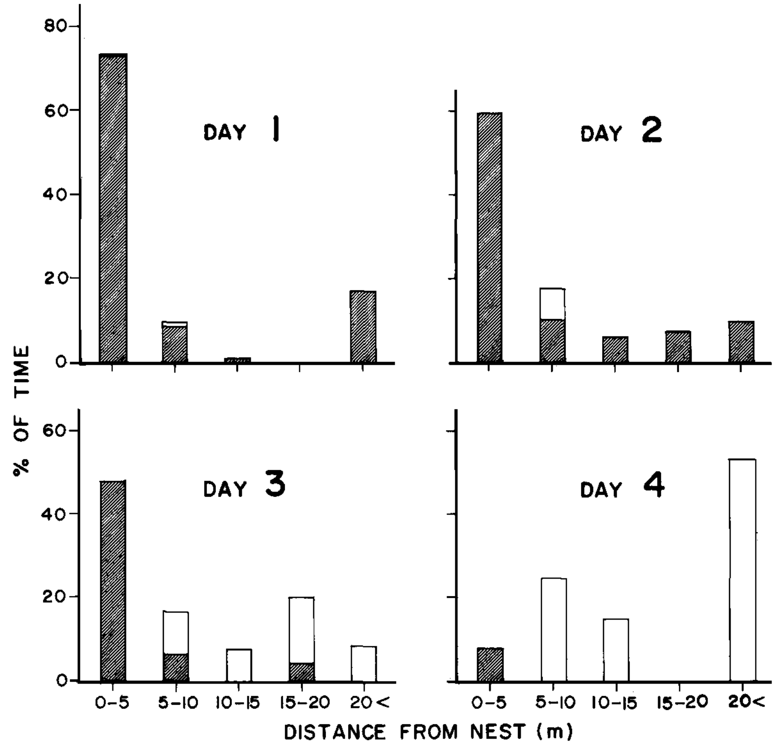

Fig. 3. Average distance of female from nest. Shaded bar shows time female spent with male and white bar shows time female spent alone.

male visits to the nest become gradually more frequent and longer as the laying period progresses. The Spotted Sandpiper male incubates sporadically before day 3 (Maxson and Oring 1980). In the Red Phalarope (Schamel and Tracy 1977, Mayfield 1979), the Wilson's Phalarope (*Phalaropus tricolor*; Howe 1975), and the Wattled Jacana (*Jacana jacana*; Osbone and Bourne 1977), males appear to begin incubating on day 3.

Consorting ratio.—A male usually followed a female for three or four days during the prelaying period. The consorting ratio was 99% in the Toyo area during the prelaying period. Although the consorting ratio for the whole laying period was 68%, it decreased from 99% on day 1 and 93% on day 2 to only 8% on the last day (Table 2). The consorting ratios varied widely among individual pairs on day 3. In two of the three pairs the female consorted with the male on day 4 only when she came to lay. One female (Nest 9), however, returned to the vicinity of the nest after laying the fourth egg and stayed within 5 m of the incubating male.

Because the male and female arrived at the nest together early in the morning before the laying of the third egg, it is possible that they had consorted during the preceding night. The female probably left her mate on the nest at night after the third egg was laid, however, because the male began spending considerable time on the nest and the female did not stay in the vicinity of the nest.

As egg laying advanced, the amount of daylight time females stayed within 5 m of the nest decreased in the Toyo area (Fig. 3). On days 1 and 2, females stayed within 5 m of the nest most of the time and consorted with the males almost all day. Within 10 m of the nest, females were occasionally separated from the males, who stayed on the nest, but when females went more than 15 m from the nest, the males always followed. On day 3 females spent less time within 5 m of the nest and often went away from the nest alone. After laying the fourth egg, females left the nest and moved solitarily, while the males stayed on the nest.

Behavior during the incubation period.—Dur-

TABLE 3. Nest attendance of male during the incubation period. (Females did not visit the nest during the incubation period.)

	Daytime	Nighttime
Average percentage time on nest (range)	80.4 (64.9–94.7)	89.6 (88.2–91.1)
Average duration of nest visits in minutes (range)	39.8 (23.9–110.4)	92.9 (77.7–111.2)
Percentage of visits exceeding 30 min	53.4	100.0
Number of days	14	2
Number of hours observed	156.0	22.6

ing the incubation period males typically left the nest 1.3 times per hour for about 10 min. Males sometimes remained on the nest for several hours, especially during the morning. At other times, they stayed away from the nest for as long as 40 min. Males were on the nest 80% of the time during the day and 89% during the night (Table 3). At night the males left the nest less frequently and spent longer periods on the nest.

When males left the nest, they usually walked or flew away immediately. In 61 of 85 observations made during the incubation period, males left the vicinity of the nest within 1 min of leaving the nest. This behavior differed markedly from behavior during the laying period, because the male spent much time in the vicinity of the nest during the laying period. A male typically flew back to a place about 20 m from the nest and then walked to the nest, where he preened for a time before entering the nest.

The incubation period averaged 16.8 days (range 16–18 days, $n = 6$). During the incubation period, the female was never seen at the nest and apparently never came anywhere near the nest (confirmed by banded females for 7 days). When the male interrupted incubation to forage, he did not consort with any females (confirmed for 6 days). The male and his chicks left the nest within a half-day after all the eggs hatched, and they never returned to their nest ($n = 4$).

DISCUSSION

In species such as the Mountain Plover (*Charadrius montanus*; Graul 1973) and the Sanderling (*Calidris alba*; Parmelee and Payne 1973), which have double clutches, females incubate the last clutch with or without males. In the polyandrous Spotted Sandpiper, females help with incubation unless they obtain a new mate (Hays 1972, Maxson and Oring 1980). On the other hand, only the males incubate in the Northern Jacana (Jenni and Betts 1978), the Red-necked Phalarope (Hildén and Vuolanto 1972), and the Red Phalarope (Mayfield 1979), all of which have proved to be polyandrous. In the Wilson's Phalarope (Howe 1975), which is probably polyandrous, only males incubate. The Painted Snipe female decreased the time she spent on the nest as egg laying advanced, and almost all her nest visits occurred before the third egg was laid and were less than 10 min long, except for the four egg-laying visits. After a male started to incubate, the female did not visit the nest again except to lay the fourth egg, nor was she ever seen in the vicinity of the nest. Therefore, incubation is performed only by a male. A female neither helps her mate nor incubates alone. This suggests that the degree of sex-role reversal in incubation is more complete in the Painted Snipe than in the Mountain Plover, the Sanderling, or the Spotted Sandpiper and is similar to that in the Northern Jacana and the three species of phalaropes. One Painted Snipe female began incubating when her mate abandoned their nest but ceased after about a half-day. This fact may suggest that ancestral Painted Snipe females incubated.

In the species in which females do not incubate, females may desert their mates during incubation, as in the Red Phalarope (Schamel and Tracy 1977, Ridley 1980); they may help their mates, as in the Northern Jacana, the females of which visit the nest, shade the eggs (Jenni and Betts 1978), and help defend the territory against other birds, even during the incubation and rearing periods (Jenni and Collier 1972, Jenni 1974); or they may desert their mates as soon as or before the clutch is completed, as in the Red-necked Phalarope (Hildén and Vuolanto 1972) and the Wilson's Phalarope (Howe 1975). In the Painted Snipe, males did not follow their mates on or after day 4, and females did not visit their nests after the fourth egg was laid. The pair bond of the Painted Snipe appeared to break down after the laying of the last egg in the same way as the pair bonds of Red-necked and Wilson's phalaropes do. It is advantageous to a sequentially polyandrous female that she desert the first mate as soon as possible and gather energy reserves sufficient to obtain the next mate and to lay his clutch. In the simultaneously polyandrous American Jacana, a female stays with her mate and prepares to lay the replacement clutch for him (Jenni and Collier 1972).

Painted Snipe females are unlikely to mate with another male during the prelaying period or on the first and second days of laying, because they consort with their current mates most of the time on these days. Females also consort with their mates during the night after the second egg has been laid. During day 3, females begin spending less time with their mates, but by this time it is likely that their fourth egg has already been fertilized. It is extremely unlikely that even the last egg could be fertilized by some other male. After laying the last egg and abandoning their mates, the females could begin to consort with other males. The abandonment of the mate and emancipation from incubation make it possible for females to mate with other males, thus enabling this species to have a sequentially polyandrous mating system.

A simultaneously polyandrous female copulates with several males in a short time. In contrast, a sequentially polyandrous female mates with only one male during a set period. The probability of a male rearing his own offspring is different in these two polyandrous sytems. In the sequentially polyandrous species, a male has only to keep his mate for a few days before and during the laying period to ensure that he will rear his own offspring (Schamel and Tracy 1977). A simultaneously polyandrous female lays the first set of eggs on one nest for the first mate and the second set of eggs on another nest for the second mate, successively (Jenni and Collier 1972, Maxson and Oring 1980), but she copulates with several males during that period. Northern Jacana females copulated with three or four different males in a single afternoon (Jenni and Collier 1972). One Spotted Sandpiper female copulated with two different males for two days, and she laid for the earlier mate on the next day. She copulated only with the later mate during the laying period of the earlier mate (Oring and Maxson 1978). In these cases, the earlier male does not always rear his own offspring, although Northern Jacana females spend a greater amount of time in the earlier male's territory just before and during the laying period and simultaneous mating is exceptional in the Spotted Sandpiper. Other mechanisms may explain fertilization in species with a simultaneously polyandrous mating system. Physiological and genetic research on these species will be necessary to identify these mechanisms.

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ENDOCRINE RESPONSES TO INCLEMENT WEATHER IN NATURALLY BREEDING POPULATIONS OF WHITE-CROWNED SPARROWS (*ZONOTRICHIA LEUCOPHRYS PUGETENSIS*)

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Abstract.—Plasma levels of luteinizing hormone (LH), testosterone, and corticosterone were measured in relation to periods of inclement versus fair weather during the reproductive season of the Puget Sound White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*). In 1974, cool stormy weather in spring delayed the onset of breeding by one month and also prolonged the period of elevated circulating levels of LH and testosterone, compared with the fair spring of 1975. Inclement weather in 1974 did not appear to be stressful, as indicated by body weights and plasma levels of corticosterone. In late May 1980, however, a storm occurred after nesting activities had begun and all pairs sampled were feeding young. In this case, plasma levels of corticosterone were greatly elevated above those of birds sampled at the same time in the warm spring of 1979 and also above those of birds sampled in spring of both 1974 and 1975. In addition, fat depots were virtually exhausted in birds sampled during the storm of 1980, suggesting that these birds were stressed. Most pairs lost their brood in May 1980, presumably to starvation, and renested after amelioration of environmental conditions in June.

These data suggest that although storms may modify the onset and temporal progression of the reproductive cycle, they are stressful to adults only when the nesting phase is in progress. Thus, the underlying mechanisms by which inclement weather delays the onset of breeding or disrupts the nesting once underway are likely to have different endocrine bases. *Received 29 March 1982, accepted 31 August 1982.*

Aseasonal storms occasionally disrupt the nesting activity of birds that breed at higher latitudes and altitudes. For example, periods of unseasonably cold weather, prolonged precipitation, or storms may reduce the trophic resources available to Chaffinches (*Fringilla coelebs*) to an extent that adults cannot find sufficient food for themselves and their nestlings. The latter may die of starvation, or, in some cases, the nest may be damaged or destroyed (Newton 1964, 1973). In Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) aseasonal snowfall may cover food resources without destroying nests. Under these conditions, breeding pairs often abandon nests, and sometimes the territory, to forage widely. As conditions ameliorate and food is again available, they return to their territories and begin a second nesting effort (Morton et al., 1972, Morton 1976). In these instances, it is tempting to suggest that aseasonal storms somehow depress circulating levels of luteinizing hormone (LH) and sex steroid hormones, which regulate sexual and territorial behavior (e.g. Adkins-Regan 1981, Harding 1981; see also Wingfield and Farner 1980), and elevate plasma levels of corticosterone, which mobilizes energy reserves (see Holmes and Phillips 1976, Siegel 1980 for reviews).

Although renesting after the loss of a clutch or brood involves well-characterized endocrine changes (Donham et al. 1976, Wingfield and Farner 1979), the effects of inclement weather and the mechanisms through which it disrupts the nesting phase are by no means clear. Storms, concomitant decreases in ambient temperature, and restricted availability of food may be stressful, especially for individuals that are incubating or feeding young. Indeed, several laboratory investigations of reproductively mature birds have shown that a variety of stresses alter temporal patterns of secretion of LH, depress plasma levels of sex steroid hormones, and elevate circulating titers of corti-

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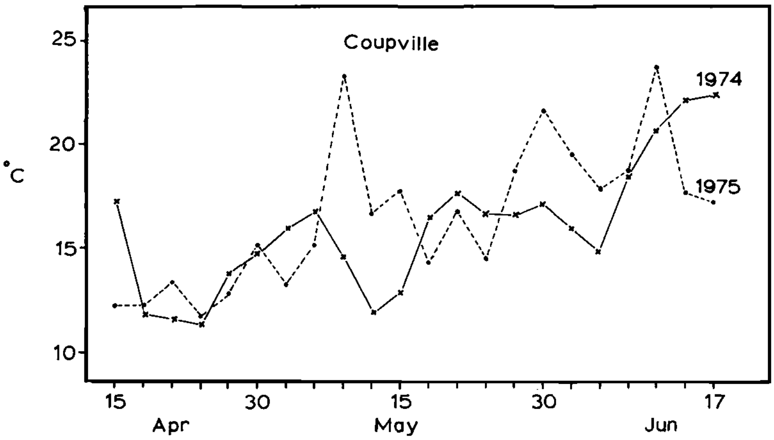

FIG. 1. Temperature data (3-day means) for Coupeville, Whidbey Island, Island County, Washington (from U.S. Environmental Data Service). Coupeville is approximately 10 km west of the study sites on Camano Island.

costerone (e.g. Wilson et al. 1979, Scanes et al. 1980, Wingfield 1980, Wingfield et al. 1982; see Holmes and Phillips 1976, Siegel 1980 for review). As far as we are aware, however, there have been no investigations of the endocrine responses of naturally breeding populations of birds to the stressful effects of aseasonal storms.

In this communication we report the effects of low ambient temperature and stormy weather on plasma levels of hormones and reproduction in free-living populations of the Puget Sound White-crowned Sparrow (*Z. l. pugetensis*).

MATERIALS AND METHODS

Study areas and field techniques.—Male White-crowned Sparrows were captured in mist nets and baited live traps in the vicinity of Seattle, Washington (48°N), on study sites on Camano Island (Island County) in 1974 and 1975 and near Hart's Lake (Pierce County) in 1979 and 1980. Results of investigations at the former site have been published previously (Wingfield and Farner 1977, 1978a).

Immediately after a bird was captured, a blood sample (approximately 400 μl) was removed from the alar vein into heparinized capillary tubes. Each bird was then banded, color marked, and weighed, and

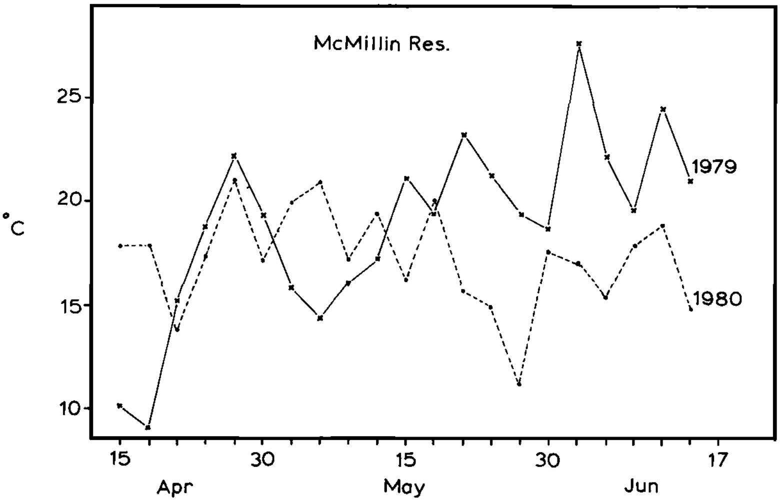

FIG. 2. Temperature data (3-day means) for McMillin Reservoir, Pierce County, Washington (from U.S. Environmental Data Service). McMillin Reservoir is approximately 25 km northeast of the study site at Hart's Lake.

TABLE 1. Breeding status in relation to weather of naturally breeding populations of White-crowned Sparrows (*Zonotrichia leucophrys pugetensis*).

Year	Sample dates	Weather	Breeding activity
1974	30 April–20 May	Cold, heavy overcast, precipitation, frequent storms	Males on territory and paired, little further breeding activity
1975	30 April–20 May	Cool, sunny, no storms	Most females incubating
1974	20 May–6 June	Cold, heavy overcast and precipitation, frequent storms	Breeding delayed by storms, very few females with nests, little breeding activity
1975	20 May–6 June	Cool, sunny, no storms	All sampled pairs feeding nestlings First fledglings appear
1974	6 June–2 July	Warm and sunny	Feeding nestlings, first fledglings appear
1975	6 June–2 July	Warm and sunny	Nesting activity for second brood, incubation and feeding nestlings
1979	26 May–31 May	Warm and sunny	All sampled pairs feeding nestlings of fledglings
1980	27 May–30 May	Cold, heavy overcast and precipitation	All sampled pairs feeding nestlings or fledglings
1980	8 July–28 July	Warm and sunny	All samples pairs feeding nestlings or fledglings

its gonadal state was assessed during unilateral laparotomy (Wingfield and Farner 1976). In 1979 and 1980, estimates of subcutaneous fat depot in the furculum and abdomen were also made. All birds were then released for field observations and possible recapture. After centrifugation of blood samples in the field, the plasma samples were frozen on dry ice until returned to the laboratory where they were stored at −20°C until analyzed (Wingfield and Farner 1976).

Collection of samples in relation to weather.—In 1974 and 1975, blood samples were collected at least 4 days per week from mid-April to August as part of an investigation of the endocrine control of reproduction under natural conditions (Wingfield and Farner 1977, 1978a). The spring of 1974 (late April and May) was marked by continually inclement weather; heavy precipitation and strong winds (up to 60 km/h) prevailed in May, in contrast with the same period in 1975 (Fig. 1).

In 1979 and 1980, blood samples were collected at least 3 days per week from mid-April through early July as part of further investigations on the hormonal control of reproduction in birds (Moore and Wingfield 1980, Moore 1982). The springs of 1979 and 1980 (April–May) were mild, with no storms, and in both years breeding began in early May. In 1980, however, an intense storm accompanied by heavy precipitation occurred at the end of May, when most pairs were feeding nestlings or fledglings. Temperature data for McMillin Reservoir, 25 km northeast of Hart's Lake, are presented in Fig. 2.

Hormone assays.—Luteinizing hormone was measured by the double antibody, post-precipitation radioimmunoassay for avian LH as developed by Follett et al. (1972) and modified for use on plasma from Passeriformes by Follett et al. (1975). Plasma levels of testosterone were measured by the methods of Wingfield and Farner (1975), and corticosterone by a radioimmunoassay procedure following the chromatographic separation procedure described by Wingfield and Farner (1975). These assays have been used routinely in this laboratory for over 8 years (see Wingfield and Farner 1977, 1978a, b, 1980).

Statistics.—Differences between groups were determined by the Mann-Whitney *U*-test, one-tailed (Zar 1974).

RESULTS

As noted above, the ambient temperature was 5–10°C lower in early May 1974 than in 1975 (Fig. 1). Early May is usually the period of egg laying for the first clutch (Fig. 1, Table 1; see also, Wingfield and Farner 1977, 1978a). Temperatures in 1974 remained generally lower than those of 1975, except for a brief period in mid-May, and did not increase appreciably until June. This period of low temperature was accompanied by heavy overcast and frequent storms with precipitation (Table 1). In 1975 weather was generally sunny and without storms; all pairs studied were feeding nestlings or fledglings by early June. In 1974 breeding was delayed, with few females having nests by this time. Nestlings were not found until late June, and the first fledglings did not appear until 2 July 1974, in comparison with 4 June in 1975.

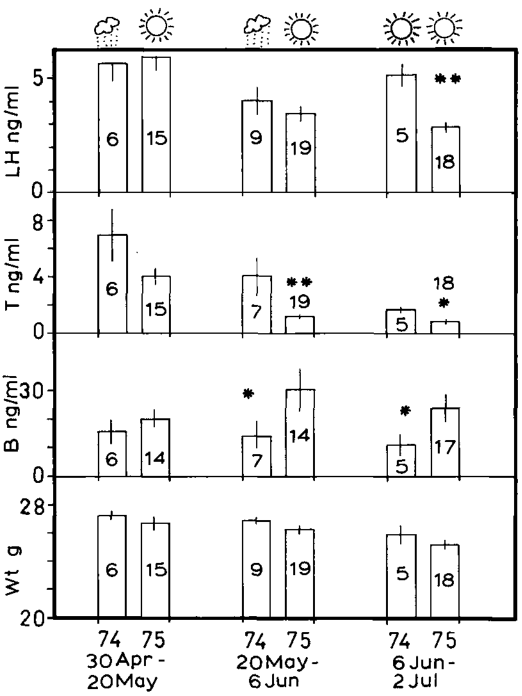

FIG. 3. Body weight, and plasma levels of LH, testosterone (T), and corticosterone (B) in male White-crowned Sparrows (*Z. l. pugetensis*) sampled during spring 1974 and 1975. The stylized rain cloud indicates the period of stormy weather, and the sun indicates periods of fair weather. Vertical lines are standard errors of means, and numbers within open bars indicate sample sizes. Asterisks indicate significant difference between 1974 and 1975, * = $P < 0.05$; ** = $P < 0.02$.

There was a downward trend in both years in plasma levels of LH and testosterone in males from late April to June or July (Fig. 3), as is typical for White-crowned Sparrows through this period (Wingfield and Farner 1977, 1978a). Plasma levels of LH in males in June 1974 were higher than in males during the same period in 1975 ($P < 0.02$), and circulating levels of testosterone were also higher during May and June in 1974 ($P < 0.02$ and $P < 0.05$). Plasma levels of corticosterone had increased by late May and June 1975 when birds were feeding young ($P < 0.05$). There were no differences in body weight between the two years.

The weather in early spring in both 1979 and 1980 was warm and sunny, with temperatures usually remaining above 15°C (Fig. 2). In both years White-crowned Sparrows were feeding nestlings or fledglings by late May (Table 1).

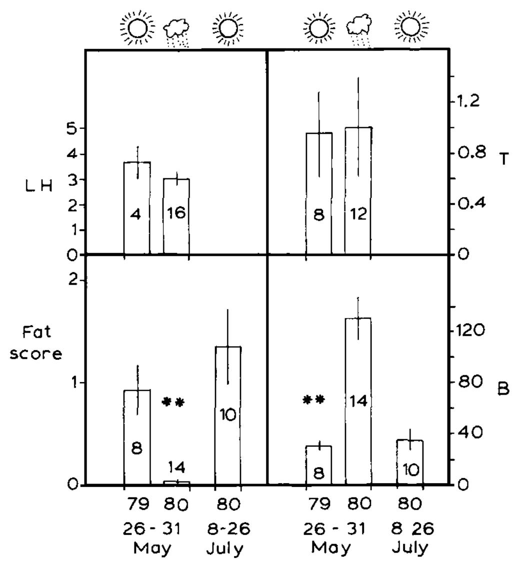

FIG. 4. Fat score and plasma levels of LH, testosterone (T), and corticosterone (B) in male White-crowned Sparrows (*Z. l. pugetensis*) sampled during spring and summer, 1979 and 1980. The stylized rain cloud indicates the period of stormy weather, and the sun indicates the periods of fair weather. Vertical lines are standard errors of means, and numbers within open bars indicate sample sizes. Asterisks indicate significant difference between 1979 and 1980, ** = $P < 0.001$.

At this time in 1980, however, there was a precipitous decrease in temperature, to as low as 10°C below that recorded at the same time in 1979 (Fig. 2), accompanied by heavy overcast and precipitation (Table 1). In June, conditions ameliorated, temperatures remaining below those of 1979 but similar to those of June 1974 and 1975 (Fig. 1). During late May 1980, plasma levels of corticosterone were elevated greatly above those of birds sampled at the same time in 1979 and at the same stage of breeding ($P < 0.001$, Fig. 4). By July 1980, when birds were feeding nestlings of a second nesting attempt, corticosterone levels had declined ($P < 0.02$). Subcutaneous fat depots were virtually depleted in birds sampled during the storm of 1980 ($P < 0.001$) but were restored by July. No differences in plasma levels of LH and testosterone in males were observed between years.

DISCUSSION

Abnormal weather conditions may delay the onset of breeding, despite the presence of functional or near functional gonads, or disrupt the nesting phase if breeding is already underway (for reviews see Marshall 1949, 1959; Lofts and Murton 1968; Farner and Lewis 1971; Newton 1973; Murton and Westwood 1977; Wingfield 1980; Wingfield and Farner 1980). Our results show that the delay in the onset of breeding caused by prolonged spring storms in 1974 was also accompanied by maintenance of elevated plasma levels of LH and testosterone, which normally decline from the initial spring peak during the onset of incubation and feeding of young (Wingfield and Farner 1977, 1978a, b). Thus, the extended period of elevated plasma levels of sex hormones in 1974 may have maintained sexual and territorial behavior so that nesting activities could begin immediately after amelioration of environmental conditions. The storms did not appear to stress the adult White-crowned Sparrows because plasma levels of corticosterone were lower than in birds sampled at the same time in 1975, when the birds were foraging intensively in order to feed young. Foraging to feed young itself may have been stressful, as suggested by the gradual increase in circulating levels of corticosterone in male *Z. l. pugetensis* during parental care (Wingfield and Farner 1977, 1978a). In 1980, however, the storm struck after the nesting phase had begun and was accompanied by a dramatic increase in plasma levels of corticosterone well above those measured in 1974 and 1975, and a decrease in subcutaneous fat depots, suggesting that these birds were stressed. Curiously, plasma levels of LH and testosterone were unaffected, probably because these levels had already declined from the initial spring peak (see Wingfield and Farner 1977, 1978a). Furthermore, these birds remained on territory (or at least in the immediate area) throughout the period of inclement weather, although nesting was generally unsuccessful, as no fledglings were observed until after a second nesting attempt in June and July.

The different endocrine responses to storms in 1974 and 1980 suggest the following explanation: If an unseasonable storm occurs early in spring, the onset of breeding is delayed even though the gonads may be functional or near functional, and plasma levels of LH and testosterone in males remain generally high. The effects of the storm do not appear to be stressful, because there are no young that require extra foraging by the adults. If storms and low temperatures occur late in spring during parental care, however, trophic resources decline at a time when both adults and a brood of young must be fed. In this case, the storm is stressful, as indicated by increases in plasma levels of corticosterone and depletion of fat stores. Thus, the underlying mechanisms by which inclement weather delays the onset of breeding or disrupts the nesting phase once underway are likely to have different endocrine bases.

Whether storms influence endocrine function through a direct effect of, for example, low temperature or an indirect effect on food resources has been a matter of conjecture (Wingfield 1980, Wingfield et al. 1982). In domestic birds low temperatures tend to depress testis growth (e.g. Huston 1975) and disrupt ovulatory cycles (e.g. Riddle and Honeywell 1924), even though food and water are provided *ad libitum*. Similar treatment also produces an elevation of circulating levels of corticosterone (Nir et al. 1975, Jeronen et al. 1976, Beuving and Vonder 1978). Low environmental temperature, however, has only a slight effect on photoperiodically induced gonadal growth in feral species (for review of early literature see Marshall 1949, see also Lewis and Farner 1973), on plasma levels of LH or testosterone, or on circulating levels of corticosterone in male *Z. l. gambelii* (Wingfield 1980, Wingfield et al. in press). Moreover, Rowan (1925) showed that male Dark-eyed Juncos (*Junco hyemalis*) housed in outdoor aviaries (in Alberta, Canada) under artificial long days and with free access to food developed functional gonads and came into full song in December, when ambient temperatures were as low as −47°C. Similarly, feral populations of crossbills (*Loxia curvirostra* and *L. leucoptera*) can breed at any time of the year if cone crops of pines (*Pinus* sp.), larches (*Larix* sp.), and spruce (*Picea* sp.) are sufficient (Bailey et al. 1953, Tordoff and Dawson 1965, Newton 1973).

Thus, if birds have free access to food, low environmental temperature appears to have little effect on reproductive function in feral species. Inanition can have rapid and dramatic effects on reproductive function, however, in both domesticated and feral avian species. For example, varying degrees of food restriction result in gonadal atrophy, decreased plasma levels of LH and testosterone, and increased concentrations of corticosterone (e.g. Assenmacher et al. 1965, Assenmacher 1973, Erb et al. 1978, Wilson et al. 1979, Harvey et al. 1980, Scanes et al. 1980, Wingfield 1980; R. A. Lewis, P. W. Mattocks, J. C. Wingfield, and D. S. Farner unpubl. results). Although low temperatures may result in more rapid depletion of energy stores, especially for nocturnal thermoregulation and for the feeding or brooding of young, these stores can be easily replaced if sufficient food is available (Ketterson and King 1977). Thus, it seems likely that inclement weather is stressful during breeding because it depresses food resources, especially in species such as the White-crowned Sparrow, which feeds its young almost entirely on insects.

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SEXUAL DIFFERENCES IN THE BEHAVIOR OF ADULT GREAT BLACK-BACKED GULLS (*LARUS MARINUS*) DURING THE PRE- AND POST-HATCH PERIODS

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ABSTRACT.—Sexual differences in the behavior of adult Great Black-backed Gulls (*Larus marinus*) were examined during the pre- and post-hatch periods of the 1980 breeding season. Following clutch completion, females invested more time than males in both territorial attendance and incubation, but there were no sexual differences in egg-shifting or grass-collection. In contrast, males engaged in more agonistic behavior and long-called and yelped in all contexts more than females before chick hatching. Males also displayed more mate-oriented mews and chokes than did females at this time. During the post-hatch period, there were no sexual differences in territorial attendance, brooding, or frequency of chick feedings, but males continued to exhibit higher frequencies of agonistic acts than did females, as well as higher levels of long-calls and yelps. After chick hatching, both sexes demonstrated increased levels of agonistic acts, long-calls, yelps, mews, and yeows, while males exhibited decreased frequencies of chokes and head-tosses. The results of this study strongly suggest that parental investment by male *L. marinus* may equal that of females. *Received 10 August 1981, accepted 28 May 1982.*

GULL species (Laridae) are generally monogamous, and members of both sexes exhibit the same behavior patterns related to parental care during the breeding season (e.g. incubation, brooding, chick feeding, territorial attendance and defense). Male and female gulls are often difficult to distinguish visually, and many descriptions of their behavioral ecology have simply "lumped" sexes in data analysis. Recent studies, however, have shown that definite differences are evident in the behavior of male and female larids. For example, Tinbergen (1956, 1960) reported that male Herring Gulls (*Larus argentatus*) were more active in collecting nest material and were involved in territorial defense more often than females. Similarly, male and female Laughing Gulls (*L. atricilla*; Burger and Beer 1975) and Ring-billed Gulls (*L. delawarensis*; Southern 1981) have been observed to exhibit differences in agonistic behavior toward territorial intruders. Male Western Gulls (*L. occidentalis*) are not only responsible for the bulk of territorial defense, but also feed chicks significantly more often than do females (Pierotti 1981). Burger (1981a) reported that, although adult male and female Herring Gulls contribute equal parental investment in the post-hatch period, sexual differences in investment patterns developed as chicks grew older. Even sexual differences in spiteful and altruistic behavior have been observed in both Herring and Western gulls (Pierotti 1980). Clearly, the investment patterns of adult larids vary qualitatively, if not quantitatively, and additional data are needed to evaluate the relative significance of male and female contributions in terms of parental effort.

We examined the behavior of adult Great Black-backed Gulls (*L. marinus*) during the incubation and post-hatch phases of the reproductive cycle. The specific objectives of this study were to: (1) investigate possible sexual differences in a number of agonistic and non-agonistic behaviors exhibited by breeding adults and (2) determine how the transition from the pre- to post-hatch periods influenced the behavior of males and females.

METHODS

This study was conducted on Little Duck Island, Hancock County, Maine between April and August 1980. Approximately 520 pairs of *L. marinus* nested

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TABLE 1. Sexual dimorphism in Great Black-backed Gulls.[a]

Sex	Weight (g)	Tarsus (mm)	Culmen (mm)	Bill depth at nares (mm)
Males ($n = 19$)	1,963 ± 11[b]	97.9 ± 0.4[b]	66.1 ± 0.6[b]	25.4 ± 0.2[b]
Females ($n = 11$)	1,577 ± 19	90.7 ± 0.7	59.7 ± 0.4	22.2 ± 0.1

[a] Data expresses as mean ± SE.

[b] Males > Females in t-test comparison, $P < 0.001$.

in two large meadows on this 35-ha island. Breeding habitat consisted of several species of grasses (*Grammineae*), stinging nettle (*Urtica dioica*), angelica (*Angelica lucida*), raspberry (*Rubus idaeus*), and exposed granite outcroppings. The island was uninhabited and supported no mammalian predators.

A blind was erected on masonary scaffolding at the periphery of the colony during the pre-incubation stage of the Great Black-backed breeding cycle. One or both adults on each of 19 nest sites were color marked with leg-streamers during the 1978, 1979, and 1980 breeding seasons (and all adults were marked with temporary dyes), all pairs were sexed on the basis of size differences, and sexes were confirmed through observed copulations. In all 19 cases, the larger member of the pair was a male, and morphometric data (see Table 1) indicated sexual dimorphism similar to that reported by Ingolfsson (1967). Study nests were selected to include sites from both high- and low-density areas within the colony (Butler and Trivelpiece 1981). Data were collected only from those territories that were entirely visible for the duration of the breeding season and those in which both members of the pair were in attendance until chicks fledged. Chicks were considered fledged at 55 days following hatching and/or when they were observed flying strongly in the vicinity of the colony.

Behavioral observations of birds on their nesting territories were conducted during daylight hours (0500–2100) over the course of the breeding season. Two observers watched an average of 10 territories on each of 18 days (1,877 nest hours) during the prehatch period and an average of 7 territories during 20 days (1,701 nest hours) of the post-hatch period. We recorded the frequencies and identities of adults engaged in the following behaviors (where necessary, definition or source of previous description for other gull species noted): upright aggressive (Fig. 1a; Moynihan 1958), grass-pull (Tinbergen 1959, 1960), face-off (behavior that occurred in an agonistic context in which one or more adults assumed a recumbant position oriented either facing or parallel to a neighboring conspecific within 1 m of a territorial boundary, possibly related to a squat-and-freeze described by Moynihan 1958), jab (gaping-jab of Moynihan 1958), charge (lunge or running approach by an adult with wings generally extended; charging bird always terminated behavior before making contact with another conspecific), chase (aerial pursuit of one adult by another), attack (physical assault upon one adult by another, which generally involved biting), fight (prolonged bout of mutual attacking), long call (Fig. 1b; Moynihan 1958, Tinbergen 1959), yelp (Fig. 1c; Stout et al. 1969, Hand 1981), mew (Fig. 1d; Tinbergen 1959, Hand 1981), yeow (plaintive call of Moynihan 1958, plaintive yeow of Hand 1981), gakker (Moynihan 1958, Eh-Eh call of Hand 1981), choke (Fig. 1e; Moynihan 1958, Tinbergen 1959), head-toss (Fig. 1f; Hand 1981), shift or roll eggs, grass-collect, feed chick, present grass to chick, and reconsume regurgitated food. In addition, the frequency and duration of time on the territory, incubation bouts, and brooding bouts were noted. Data collection was facilitated by our use of binoculars (10×), digital stopwatches, cassette tape-recorders, and super-8 mm movie cameras. We determined territorial boundaries by means of aerial photographs taken in May 1980 and measurements made with an optical tape measure (see Butler and Janes-Butler 1982).

For the purpose of examining sexual differences in behavior, frequency scores from each adult pair were analyzed using the Wilcoxon signed-ranks test. Intrasexual comparisions between the pre- and post-hatch periods were analyzed in the same fashion. Proportional differences were treated with the Chi-square statistic applied to raw data rather than percentages. Morphometric data were analyzed using the t-test. To facilitate analysis and discussion, behavioral data were broken down into acts related either to attendance and care of offspring, intrapair behavior, or agonistic interactions. Behaviors such as the long-call, which occurred in each of the above categories, were analyzed according to their contextual appearance.

RESULTS

Attendance and care of offspring.—Before their chicks hatched, adult females were observed occupying territories ($t = 51.1$, $n = 19$, $P < 0.05$) and incubating ($t = 32.0$, $n = 19$, $P < 0.005$; Fig. 2) significantly more than were males. There were no differences, however, between males and females in the mean (±SE) frequencies of egg-shifting ($\bar{x} = 0.30 \pm 0.05$/h

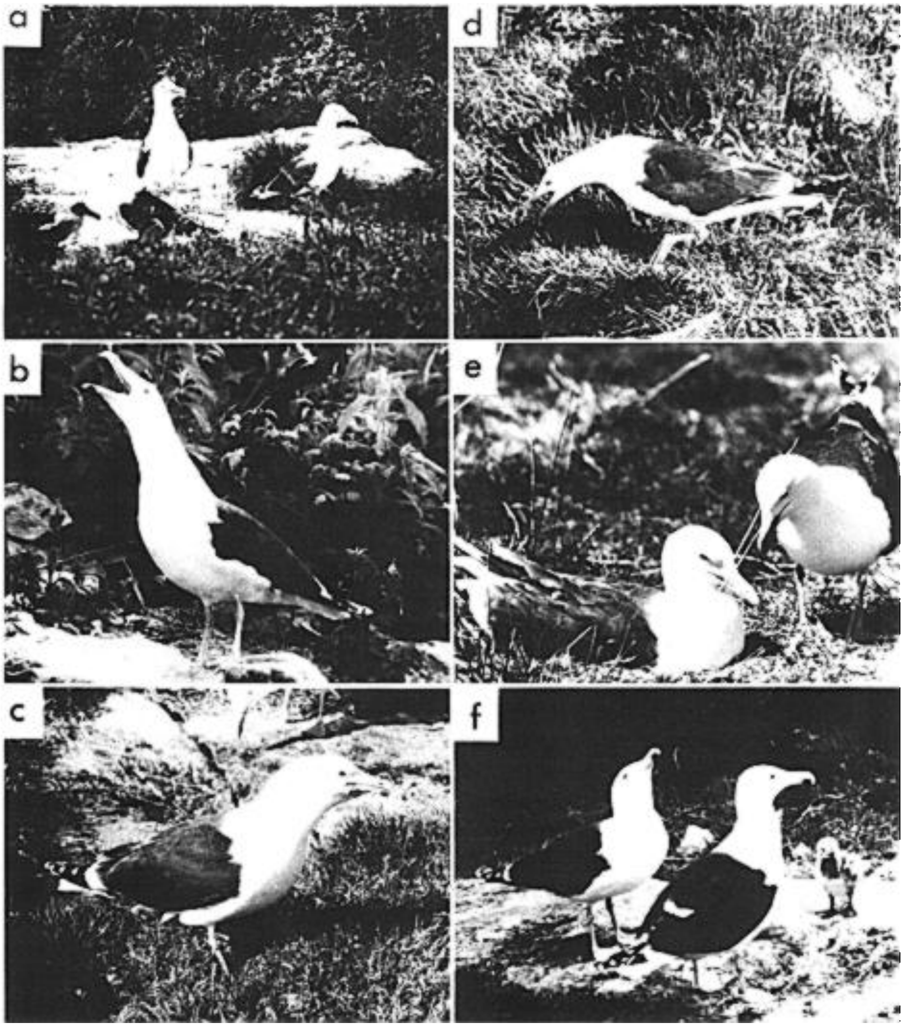

Fig. 1. Behavior patterns in which male and female Great Black-backed Gulls differed over the course of the breeding season: (a) upright aggressive (and gakker) by several adults near territorial boundary, (b) long-call, (c) yelp, (d) mew, (e) choke by pair following grass presentation by standing bird, (f) head-toss (adult female on left) before regurgitation by mate to chick.

and 0.34 ± 0.04/h, respectively) or bouts of nest-substrate collecting ($\bar{x}$ = 0.18 ± 0.05/h and 0.14 ± 0.08/h, respectively). The mean nest-relief interval was 5.3 ± 0.6/h, and males fed females at the nest site only infrequently following clutch completion ($\bar{x}$ = 0.007 ± 0.006/h). Following chick hatching, males and females did not differ in terms of time in attendance on the territory, and both sexes participated equally ($\bar{x}$ = 13 ± 5 min/h and 18 ± 5 min/h, respectively) in brooding chicks during the first week following hatching (Fig. 2).

Males and females did not differ significantly in terms of which hours of the day they were in attendance during either the pre- or post-hatch periods. The overall adult attendance pattern did change, however, following hatching (Fig. 3). During the pre-hatch period, maximum numbers of adults were in attendance on territories during early morning, late afternoon, and evening hours, and territories were generally left unattended for no longer than 1–2 min. During these brief absences, the adult in attendance generally flew out over the col-

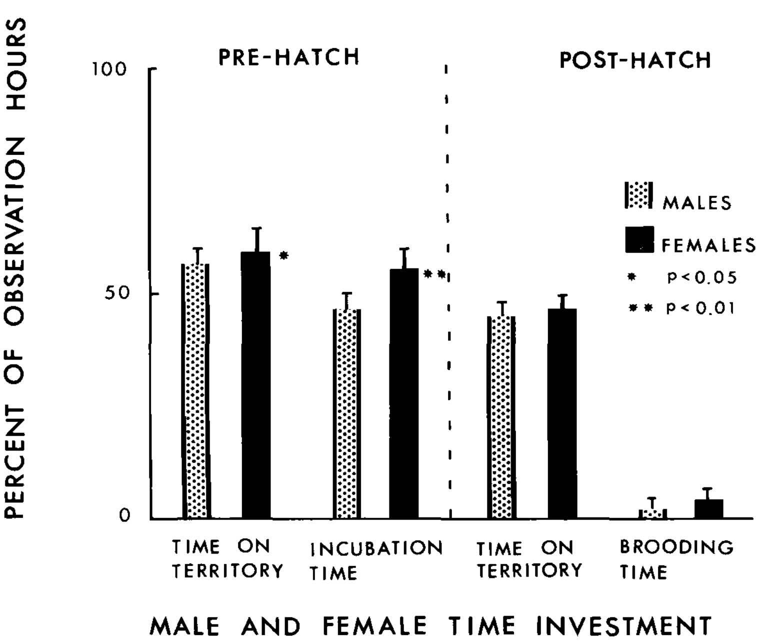

Fig. 2. Pre-hatch (1,877 nest-hours) and post-hatch (1,701 nest-hours) comparisons of male and female time investment in territorial attendance, incubation, and brooding. Significant Chi-square values for intersexual comparisons (*) are indicated.

ony, defecated, and then returned to incubate. In contrast, during the post-hatch period, one or sometimes both mates left the territory in early morning (presumably to forage to feed their chicks), and maximal numbers of adults were observed on the territories only in late afternoon and evening. Temporary adult desertion of territories increased steadily from 0.2% of the total observation hours in the first 10 days of June to 46.3% of the observation hours in the last 10 days of July. Some chicks were left unattended for periods of up to 8 h, and presumably both adults were out foraging at these times. Although this pattern varied between high- and low-density nesting areas (Butler and Janes-Butler 1982), there were no sexual differences in the proportion of time spent away from the territory by pairs in these areas. Attendance patterns during both the pre- and post-hatch periods in 1980 were not affected significantly by the occurrence of high and low tides. This may be related to the fact that, during 1980 breeding season, over 87% of the food items identified (47% of all chick feedings) consisted of fish [alewife (*Pomolobus pseudoharengus*), herring (*Clupea harengus*), lumpfish (*Cyclopterus lumpus*), mackeral (*Scombar scombrus*), sculpin (*Myoxocephalus* sp.), and unidentified fish remains] or pelagic invertebrates [krill species and squid (*Loligo borealis*)], organisms relatively independent of tidal cycles. There were no sexual differences in the types of food items fed to chicks. Males and females did not differ in mean frequencies of chick feedings ($\bar{x}$ = 0.50 ± 0.06/h and 0.45 ± 0.06/h, respectively), reconsumption of food offered to chicks ($\bar{x}$ = 0.12 ± 0.04/h and 0.13 ± 0.03/h, respectively), or presentation of grass or other substrate to chicks ($\bar{x}$ = 0.13 ± 0.03/h and 0.17 ± 0.05/h, respectively).

Adult vocalizations that were directed at chicks included long-calls, mews, and yelps. Chicks that mandibulated the bills of recumbant adults and/or continuously solicited feedings often elicited long-calls from their parents. Adults also long-called when chicks left the territory and/or when they returned to the territory, especially if neighboring adults were in the area. Males long-called more than females in this context ($t = 32.5$, $n = 19$, $P < 0.01$). Adults yelped and mewed most often before feeding chicks. These vocalizations were also

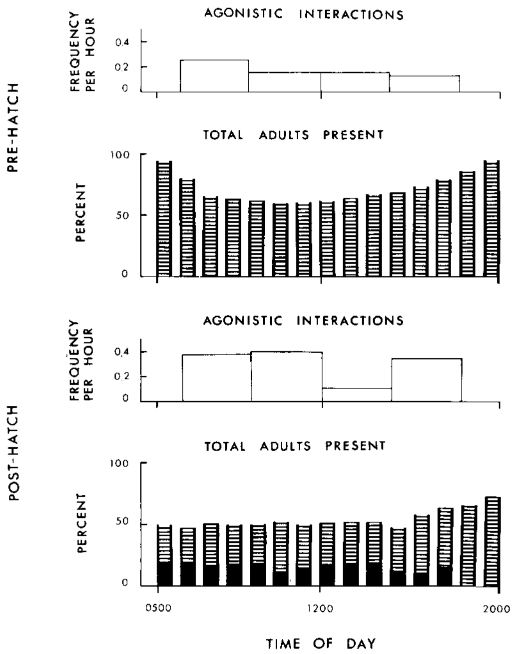

Fig. 3. Diurnal changes in both territorial attendance (expressed as percentage total adults in attendance) and the mean frequencies of agonistic acts for adult gulls during the pre- and post-hatch periods. Blackened portions of attendance bars represent percentage of territories left unattended during the post-hatch period.

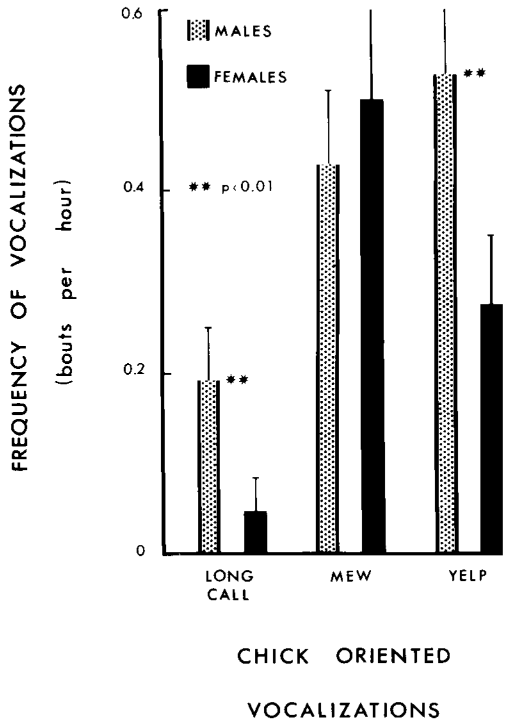

Fig. 4. Comparisons of mean frequencies of chick-oriented vocalizations exhibited by adult males and females. Results of Wilcoxon signed-ranks tests for intersexual comparisons (*) are indicated.

used by adults, however, when chicks were out of sight in dense vegetation or when chicks wandered too close to a territorial boundary or a neighboring adult. Males yelped significantly more often than females ($t = 29.5$, $n = 19$, $P < 0.01$), but there were no sexual differences in the frequency of chick-oriented mews (Fig. 4).

Pair-bond related behavior.—Adults directed long-calls, mews, yelps, chokes, and head-tosses at their mates during both the pre- and post-hatch periods (Fig. 5). Long-calls were generally given to or by landing mates, and males long-called more than females during both the pre-hatch ($t = 35.0$, $n = 19$, $P < 0.01$) and post-hatch periods ($t = 41.5$, $n = 19$, $P < 0.025$). Both males and females exhibited increased frequencies of mate-directed long-calls following chick hatching ($t = 30$, $n = 19$, $P < 0.005$ and $t = 0$, $n = 19$, $P < 0.005$, respectively). Mate-oriented mews and chokes, and to a lesser extent head-tosses, appeared primarily in the context of nest relief in both sexes. Head-tossing also appeared in the context of limited mate feeding during the early pre-hatch periods, as well as during attempts by females to eat food being presented by males to their chicks during the post-hatch period. There were no sexual differences in head-tossing during the pre-hatch period (Fig. 5), but males mewed ($t = 46.0$, $n = 19$, $P < 0.025$) and choked ($t = 28.5$, $n = 19$, $P < 0.01$) more than their mates. Both sexes exhibited significant decreases in mate-directed mews following hatching (males: $t = 13.0$, $n = 19$, $P < 0.005$; females: $t = 18.0$, $n = 19$, $P < 0.005$), but only males choked ($t = 53.5$, $n = 19$, $P < 0.05$) and head-tossed significantly less frequently ($t = 25$, $n = 19$, $P < 0.005$) during this period. Finally, males and females yelped before their own or their mate's aerial departure from the territory. Males yelped in this context significantly more often than females, however, both before ($t = 19.5$, $n = 19$, $P < 0.005$) and after ($t = 11.5$, $n = 19$, $P < 0.005$) chick hatching. Intrasexual comparisons of yelps before and after hatching revealed no significant changes (Fig. 5).

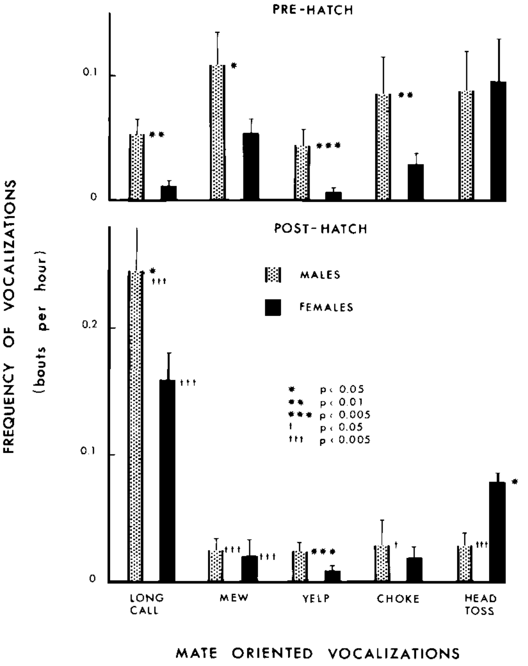

Fig. 5. Pre- and post-hatch comparisons of mean frequencies of mate-oriented vocalizations exhibited by adult males and females. Results of Wilcoxon signed-ranks tests for intersexual comparisons (*) and intrasexual comparisons between the pre- and post-hatch periods (†) are indicated.

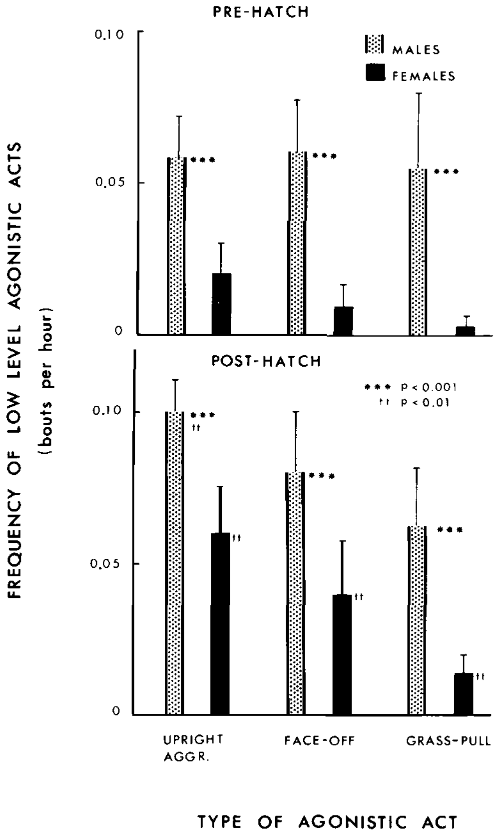

Fig. 6. Pre- and post-hatch comparisons of the mean frequencies of low-level agonistic acts by adult males and females. Results of Wilcoxon signed-ranks tests for both intersexual comparisons (*) and intrasexual comparisons between the pre- and post-hatch periods (†) are indicated.

Agonistic behavior.—Agonistic interactions accounted for 34% of all social interactions during the pre-hatch period and 35% of all encounters during the post-hatch period. Males and females exhibited marked sexual differences in agonistic behavior during both periods (Fig. 6 and 7). During the pre-hatch period, males exhibited significantly greater frequencies of low-level agonistic acts than did females, including upright aggressive displays ($t = 13.5$, $n = 19$, $P < 0.001$), face-off encounters ($t = 12.0$, $n = 19$, $P < 0.001$), and grass-pulling bouts ($t = 12.0$, $n = 19$, $P < 0.001$; Fig. 6). There were no statistical differences in frequencies of high-level agonistic acts in the pre-hatch phase of the breeding cycle. During the post-hatch period, males again displayed significantly greater frequencies of upright aggressive behavior ($t = 27.5$, $n = 19$, $P < 0.01$), face-off interactions ($t = 36.5$, $n = 19$, $P < 0.01$), and grass-pulling bouts ($t = 12.0$, $n = 19$, $P < 0.001$; Fig. 6). Males also charged conspecifics significantly more often than did females ($t = 36.0$, $n = 19$, $P < 0.01$), although there were no other significant differences in frequencies of high-level agonistic acts following chick hatching (Fig. 7). The frequency of fights that males ($\bar{x} = 0.005 \pm 0.004$/h) and females ($\bar{x} = 0.002 \pm 0.002$/h) engaged in did not differ significantly.

Intrasexual comparisons of the pre- and post-hatch phases indicated that, following hatching, males demonstrated significantly higher levels of upright aggressive behavior ($t = 28.5$, $n = 19$, $P < 0.005$), charges $t = 35.5$, n = 19, $P < 0.01$), and chases ($t = 0$, $n = 19$, $P < 0.001$; Figs. 6 and 7). Females showed changes only in the frequency of low-level agonistic acts during the post-hatch period. These included significant increases in upright aggressive acts ($t = 18.5$, $n = 19$, $P < 0.005$), face-off behav-

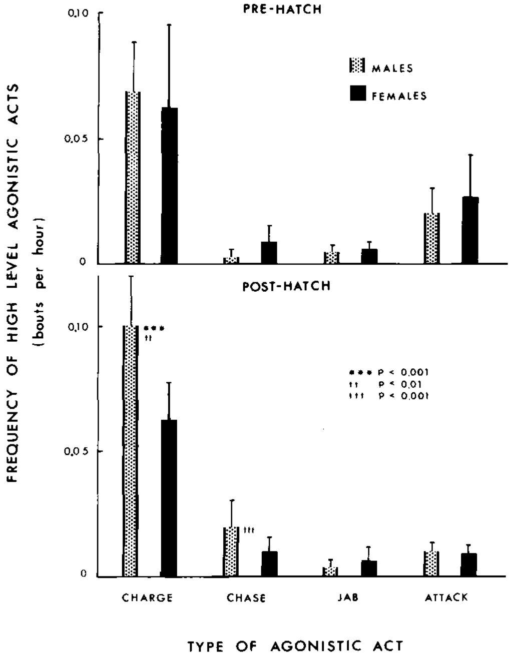

Fig. 7. Pre- and post-hatch comparisons of the mean frequencies of high-level agonistic acts for adult males and females. Results of Wilcoxon signed-ranks tests for both intersexual comparisons (*) and intrasexual comparisons between the pre- and post-hatch periods (†) are indicated.

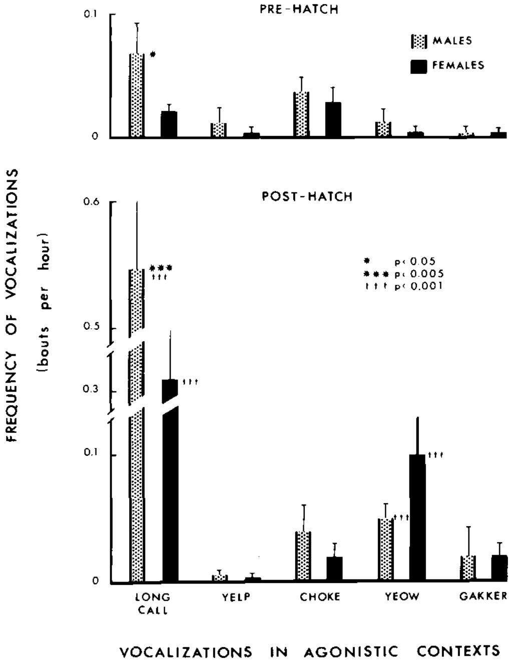

Fig. 8. Comparisons of pre- and post-hatch mean frequencies of vocalizations that were exhibited by adult males and females in agonistic contexts. Results of Wilcoxon signed-ranks tests for both intersexual comparisons (*) and intrasexual comparisons between the pre- and post-hatch periods (†) are indicated.

ior ($t = 36.5$, $n = 19$, $P < 0.01$), and grass-pulling ($t = 25.0$, $n = 19$, $P < 0.01$; Fig. 6). The frequencies of agonistic behavior displayed by both sexes showed an abrupt and sustained increase over the course of the entire post-hatch period. Examination of the daily occurrence of agonistic interactions from 0600 to 0900, 0900 to 1200, 1200 to 1500, and 1500 to 1800 revealed no substantial differences during the pre-hatch period (Fig. 3). Following hatching, however, a distinct decrease in agonistic interactions for both sexes was observed between 1200 and 1500 (Fig. 3). This decrease corresponded to generally higher ambient temperatures and the tendencies for both adults and chicks to sleep or remain inactive during these periods.

Vocalizations that were frequently exhibited by adult gulls in agonistic contexts included the long-call, yelp, choke, yeow, and gakker. The long-call, yelp, and choke occurred most frequently during conspecific overflights of the territory, during interactions involving adjacent territory holders, when a neighboring adult landed on its own territory, when other adults gave long-calls or yelps, when two or more neighboring territory holders that shared a common boundary with a calling gull interacted, or at times in response to a non-neighboring intruder before a more high-level response by the territory holder. The yeow and gakker, which appeared to function more as alarm or alerting calls, were observed most often when a high-level agonistic interaction was in progress near the territorial boundary of the calling bird, when adults and chicks from two different territories were in close proximity near their mutual boundaries, when the calling bird's chick was in an adjacent territory, when a calling bird was intruding into an adjacent territory, or on windy days when large numbers of adults were soaring over a calling gull's territory. During the pre-hatch period, males displayed significantly higher frequencies of long-calls than their mates ($t = 51.5$, $n = 19$, $P < 0.05$) but did not differ with regard to oth-

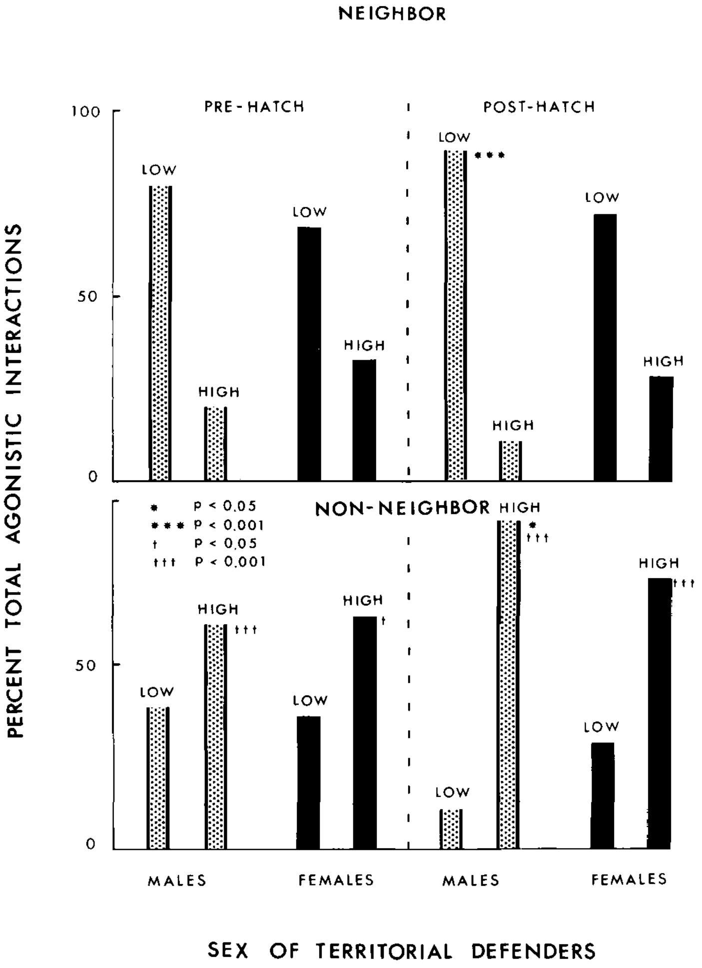

Fig. 9. Percentage of low- and high-level agonistic interactions between neighboring and non-neighboring intruders and adult males (total of 442) and females (total of 192), during the pre- and post-hatch periods. Results of Chi-square tests for both intersexual comparisons (*) and intrasexual comparisons between the pre- and post-hatch periods (†) are indicated.

er agonistic vocalizations (Fig. 8). Similarly, during the post-hatch period, males showed significantly higher frequencies only of long calls ($t = 4.0$, $n = 19$, $P < 0.001$). Both males and females displayed intrasexual increases in the frequencies of both long-calls (males: $t = 0$, $n = 19$, $P < 0.001$; females: $t = 0$, $n = 19$, $P < 0.001$) and yeows (Males: $t = 12$, $n = 19$, $P < 0.001$; females: $t = 11$, $n = 19$, $P < 0.001$) following chick hatching (Fig. 8).

Males and females also displayed some differences in agonistic behavior related to territorial defense, depending on both the sex and type of intruder (i.e. neighbor or non-neighbor). Both males and females displayed significantly more high-level agonistic responses to non-neighboring intruders than to neighboring intruders during both pre- ($\chi^2 = 29.56$, df = 1, $P < 0.001$ and $\chi^2 = 6.06$, df = 1, $P < 0.05$, respectively) and post-hatch periods ($\chi^2 = 147.22$, df = 1, $P < 0.001$ and $\chi^2 = 26.07$, df = 1, $P < 0.001$, respectively; Fig. 7). During the post-hatch period, however, males displayed a significantly greater proportion of low-level responses to neighbors ($\chi^2 = 11.58$, df = 1, $P < 0.001$) and high-level responses to non-neighbors ($\chi^2 = 4.68$, df = 1, $P < 0.05$) than did females (Fig. 9). Comparisons of the pre- and

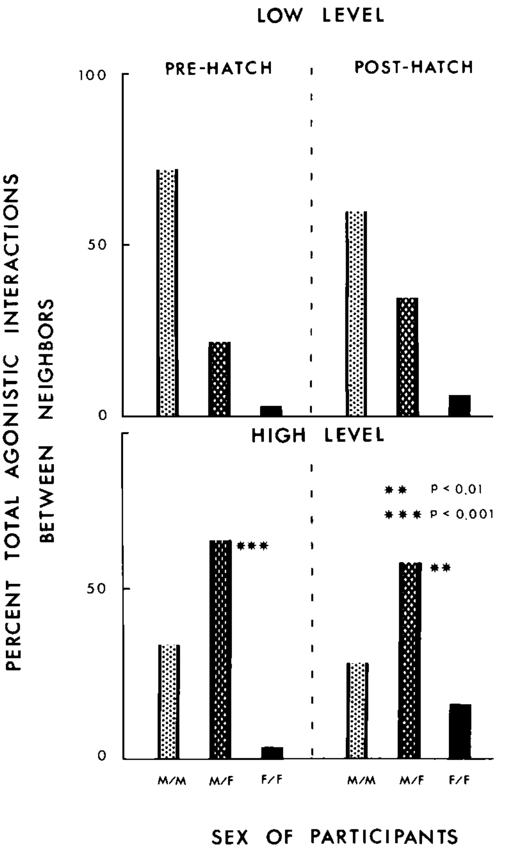

Fig. 10. Percentage of low- and high-level territorial interactions that occurred between three possible dyads; M/M = male-male (240 interactions), M/F = male-female (147 interactions), F/F = female-female (27 interactions). Results of Chi-square tests of comparisons (*) of the distribution of low- and high-level interactions between the pre- and post-hatch periods are indicated.

post-hatch periods revealed no significant changes in the frequencies of intrusions by either neighboring ($\bar{x} = 0.12 \pm 0.03$/h and 0.16 ± 0.04/h, respectively) or non-neighboring conspecifics ($\bar{x} = 0.08 \pm 0.02$/h and 0.10 ± 0.03/h, respectively).

Analysis of agonistic interactions between neighboring territorial adults (in which the sexes of both members of a dyad could be identified) indicated that, during the pre- and post-hatch periods, low-level agonistic interactions occurred primarily between males and high-level encounters occurred most often between male and female defenders ($\chi^2 = 14.89$, df = 1, $P < 0.001$ and $\chi^2 = 11.93$, df = 1, $P < 0.01$, respectively; Fig. 10). Female-female interactions were rare and accounted for only 6% of the agonistic encounters between neighboring pairs. These data reflect the type of response directed at approaching males and females by defenders of the same or opposite sex regardless of the phase of the breeding cycle. Males approaching or intruding within a territorial boundary generally elicited a low-level agonistic act from defenders of either sex. Approaching or intruding females, however, were significantly more likely to stimulate a high-level response (e.g. attack, charge, or chase) by both males ($\chi^2 = 19.69$, df = 1, $P < 0.001$) and females ($\chi^2 = 5.16$, df = 1, $P < 0.05$; Fig. 11).

Pre- and post-hatch comparisons of male and female reactions to the involvement of their mates in an agonistic interaction (while both members of the pair were in attendance) revealed significant increases in the proportion of agonistic responses by both males ($\chi^2 = 6.46$, df = 1, $P < 0.05$) and females ($\chi^2 = 6.03$, df = 1, $P < 0.05$). In addition, males were much more likely to exhibit agonistic responses to aggressive interactions involving their mates than were females ($\chi^2 = 4.93$, df = 1, $P < 0.01$). Male involvement in these mate-neighbor interactions was often closely preceded or followed by the female mate's withdrawal and mewing return to the vicinity of the chicks. Intermate agonistic interactions were infrequent and generally involved a male attacking its mate as she attempted to eat food regurgitated by the male to its chicks. Females were never observed attacking their mates under similar circumstances.

Discussion

The results of the present study of adult Great Black-backed Gulls indicate that: (1) females invested more time than males in territorial attendance and incubation during the pre-hatch period; (2) there were no sexual differences in other types of offspring care or in territorial attendance during the post-hatch period; (3) males were more aggressive than females throughout the season; (4) both males and females displayed increased investment in agonistic behavior during the post-hatch period, as well as increased levels of long-calls and yeows in agonistic contexts; and (5) both sexes showed a significant increase in the use of long-calls, yelps, and mews in offspring-oriented contexts.

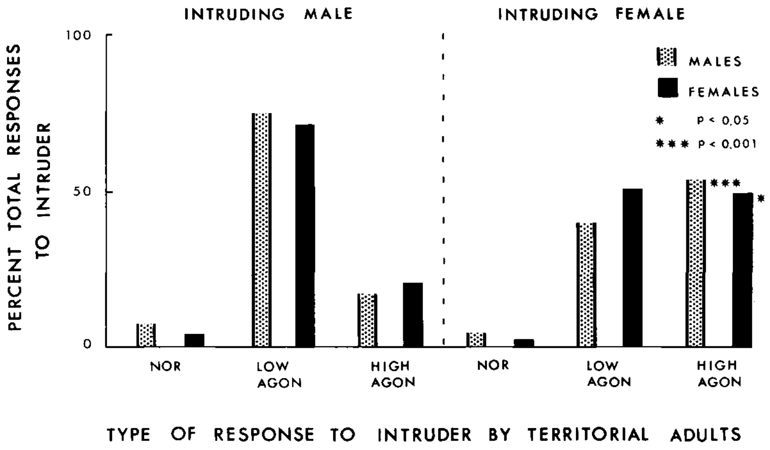

Fig. 11. Type of response (NOR = no obvious response, low-level agonistic, or high-level agonistic) directed at intruding males and females by defending adults. Results of Chi-square tests of comparisons (*) of the distribution of responses directed at intruders by males (317 responses) and females (114 responses) are indicated.

Agonistic behavior is an important investment for adults during the breeding season, due to the potential risk of injury during high-level agonistic interactions. Although attacks and fights are relatively rare, some adults do sustain eye and wing injuries during such encounters (pers. obs.). When compared with their mates, males consistently displayed higher frequencies of agonistic behavior, were more likely to exhibit high-level agonistic behavior towards non-neighboring intruders and female neighbors, generally exhibited an aggressive response to agonistic interactions between their mates and other adults, and were always dominant over their mates during interpair, agonistic interactions. Pierotti's (1981) observations of female Western Gulls attempting to relieve their mates on the nest in response to the landing of an intruder concurs with our post-hatch data concerning similar situations involving *L. marinus* pairs. This phenomenon may actually represent a "manipulation" on the part of the female for further investment by the male. In fact, increased aggressiveness on the part of male gulls may extend throughout the year, as Monaghan (1980) observed that male Herring Gulls were dominant over females and juveniles during feeding interactions in winter months. The relative risk to territory holders of engaging in agonistic interactions with normally more aggressive males may be reflected in the fact that intruding males generally elicited low-level responses from neighboring defenders of either sex, while female intruders were more likely to stimulate high-level responses. The increased frequency of agonistic acts, as well as vocalizations given in agonistic contexts, by both sexes during the post-hatch period was probably associated with movements of chicks within the natal territory, the presence and movements of chicks (and corresponding movements of adults) on neighboring territories, the relative increase in the number of adult overflights related to foraging trips to feed chicks, and/or the increased investment adults have in older offspring. Previously reported post-hatch increases in territory size in Glaucous-winged Gulls (*L. glaucescens*) (Hunt and Hunt 1976), Herring Gulls (Burger 1980), and Great Black-backed Gulls (Butler and Janes-Butler 1982) are also probably related to increased offspring mobility.

Any explanation of sexual and seasonal differences in vocalizations (and their associated behavior patterns) necessitates some interpretation of their functional significance. This is sometimes difficult, because gull displays and vocalizations may have multiple, context-dependent messages and meanings (Beer 1975, 1980), and it is not always possible to determine context definitively. Choking, mewing, yelping, and long-calling occurred in a variety of contexts over the course of the breeding cycle. Greater pre-hatch frequencies of male mewing and choking (in mate-oriented contexts) may

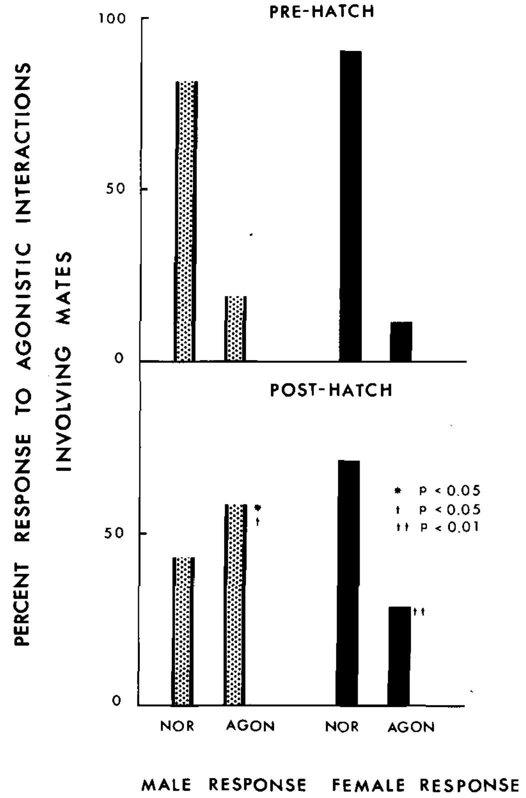

Fig. 12. Type of response (no obvious response = NOR or agonistic response) of adult males (42 responses) and females (108 responses) to agonistic interactions involving their mates. Results of Chi-square tests for both intersexual comparisons (*) and intrasexual comparisons between the pre- and post-hatch periods (†) are indicated.

have been related to increased time investment by females in incubation and corresponding increased nest-relief attempts by males. The post-hatch increases in frequency of both mewing and yelping by both sexes were probably related to a major shift from agonistic and mate-related encounters to parent-offspring interactions. Both vocalizations (often given in combination) appeared in function to attract and/or locate chicks before feeding, when a chick was separated from the adult(s) in dense vegetation, when a chick had wandered out of its natal territory, or when a chick was in the vicinity of a neighboring adult. Evans (1980) has suggested that parent-chick recognition of individually distinctive mew calls in Ring-billed Gulls is reinforced through feeding, and the same may be true of the yelp of *L. marinus* in this context. Although the significance of consistent sexual differences in yelping and long-calling during both the pre- and post-hatch periods remains unclear, the use of the latter in terms of advertisement and individual identification (Beer 1975, 1980), as well as the possible function of the yelp in this context, should not be overlooked. Stout's (1975; Stout et al. 1969) observations that the yelp of Glaucous-winged Gulls followed the termination of agonistic interactions are not inconsistent with this suggested function.

Gakkering and yeowing in Great Black-backed Gulls both appeared to function as alert/alarm vocalizations. Gakkering occurred frequently in agonistic contexts. It was also observed, however, when a human intruder approached the colony. Adults generally yeowed in response to high-level agonistic interactions nearby or when a chick wandered into the vicinity of a neighboring adult. This vocalization also was given in response to human intrusions into the colony, however, and during rare overflights of Ravens (*Corvus corax*). Both vocalizations appeared to be highly socially facilitated and often resulted in alerting large portions of the colony. The typical chick's response to these calls was to walk quickly out of sight into dense vegetation on the territory. We suggest that the post-hatch increase in frequence of yeowing was related to the increased vulnerability of mobile offspring to both conspecific aggression and predation.

Head-tossing and its accompanying vocalization have typically been ascribed the function of food-begging in female gulls during courtship (Tinbergen 1959, 1960). Smith (1980) has recently suggested that this type of behavior is actually an investment "demand" on the part of the females of some monogamous species. In *L. marinus* adults, males typically fed females during the pre-egg period, but both members of the pair exhibited head-tossing during the initial phases of courtship-feeding sequences. The behavior persisted in both sexes throughout the incubation period (even though courtship-feeding did not) and was most frequently observed when one adult joined its mate on the territory. Following chick hatching, the frequency of male head-tossing declined significantly, but females generally displayed this behavior during chick-feeding by the male. Continued female head-tossing following chick hatching may represent further "manipulation" of males that facilitates close approach of their mates to the site of chick feedings. Males did not generally react aggressively to approaching females that displayed head-tossing, although males often rapidly reconsumed food packages under these circumstances. Females were jabbed at or attacked by their mates only when they attempted to consume the food regurgitated for chicks. Females that obtained food in this manner were often observed feeding chicks themselves within an hour.

Trivers (1972) defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." In this regard, much of the behavior displayed by an adult during the incubation and chick phases of the reproductive cycle (other than those that promote adult survival) may be considered investment in offspring. Trivers hypothesized that females (due to the larger size of their gametes) already have a greater investment in their offspring at fertilization and therefore should be willing further to invest more energy than males in parental care. Gladstone (1979), however, has questioned the actual "cost" of female gamete production relative to male energy expenditures and risks with regard to such activities as territorial defense. In fact, recent studies of the breeding biology of Northern Gannets (*Morus bassanus*; Montevecchi and Porter 1980) and Black Skimmers (*Rynchops niger*; Burger 1981b) have stated that male parental investment may equal or actually exceed that of females. Care must be taken, however, in designating behavioral acts related to reproductive effort as either parental investment or mating effort. For example, male territorial defense before clutch completion may aid in avoidance of cuckoldry, and agonistic behavior during this period would be considered primarily mating effort.

Moreover, interpretations of the relative investments of males and females in their offspring must be formulated cautiously because of the difficulty of equating such factors as the cost of gamete production, time spent in territorial attendance and incubation, the energy and risks involved in agonistic behavior, and future benefits accrued from territorial defense by site-tenacious species. Due both to the facts that data in the present analysis were collected after clutch completion and that territorial defense appears to be related to chick survival (Butler and Janes-Butler 1982), we considered agonistic behavior of Great Black-backed Gulls in this study to be primarily parental investment. Although *L. marinus* females did invest statistically more time than males in territorial attendance (67% and 59%, respectively) and incubation (57% and 43%, respectively), these differences were small, and the activities involved were relatively risk-free. In contrast, males appeared to maximize their parental effort by investing significantly more in agonistic behavior than did females during both the pre- and post-hatch periods. In the absence of sexual differences in other types of parental care (e.g. post-hatch attendance, brooding, chick-feeding, etc.), the results of the present study strongly suggest that parental investment by male Great Black-backed Gulls may equal that of females. Pierotti (1981) observed a similar investment pattern in Western Gulls, but further investigation will be necessary to confirm whether this is typical for larids in general.

ACKNOWLEDGMENTS

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NEST MICROCLIMATE, WATER-VAPOR CONDUCTANCE, AND WATER LOSS IN HERON AND TERN EGGS

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ABSTRACT.—Rates of water loss ($\dot{M}_{H_2O}$) were measured in eggs of seven species of tree-nesting Ciconiiformes and three species of ground-nesting Charadriiformes during natural incubation. Measurements of egg temperature, conductance of the egg shell to water vapor, and nest and ambient humidity allow one to calculate the difference in water-vapor pressure (ΔP) between egg and nest and between nest and ambient air. ΔP between egg and nest was significantly lower in ground-nesting species (23 torr) than in tree-nesting species (31 torr). We suggest that low ΔP in ground-nesting species was due to relatively high humidity (ca. 27 torr) in nests built on the ground compared to the humidity in loose stick nests of tree-nesting species (ca. 14 torr). Water-vapor conductance of eggs from more humid nests is relatively higher than that of eggs from less humid nests (107% and 78% of predicted values, respectively), resulting in similar fractional losses in mass for the whole incubation period in both groups of birds. $\dot{M}_{H_2O}$ was not always constant throughout incubation. We suggest that changes in $\dot{M}_{H_2O}$ may be due to changes in ambient humidity and/or egg temperature. *Received 29 December 1980, resubmitted 5 January 1982, accepted 5 July 1982.*

AVIAN eggs lose water by diffusion through pores in the shell. Total water loss during incubation must be within certain limits for successful development. Hatchability of chicken eggs is optimal when total water loss is 10–12% of initial egg mass (Lundy 1969), and water loss of naturally incubated eggs of a wide variety of birds averages about 15% (Drent 1975, Ar and Rahn 1980). The rate of water loss from eggs is determined by: (1) the pore geometry (length, cross-sectional area, and number of pores) of the eggshell, which determines water-vapor conductance; (2) egg temperature, which determines water-vapor pressure within the egg; and (3) parental behavior, nest structure, and ambient conditions, which interact to determine water-vapor pressure in the nest.

We investigated the interaction of these factors in the water economy of 10 species of birds. Although all the species studied nest in colonies on small islands off the coast of North Carolina, their nesting habits fall into two distinct categories. The herons, egrets, and ibis build their nests in trees, usually 2–5 m above the ground. Their nests consist of loosely woven sticks and twigs and are sometimes so flimsy that the eggs can be seen through the bottom of the nest. The terns and gulls nest on the ground. The terns lay their eggs in a scrape on exposed sand, whereas the gulls construct nests of vegetation that are usually placed under cover of grass or small shrubs.

We measured rates of water loss and water-vapor conductance of naturally incubated eggs in each species and also measured egg temperature, nest humidity, and ambient humidity in four of these species. Results of this study suggest that the difference in water-vapor pressure between an egg and its microenvironment is less in the ground nests of gulls and terns than it is in the tree nests of herons.

MATERIALS AND METHODS

Birds and study area.—We studied eggs of 7 species of herons, egrets, and ibis (Table 1), and 3 species of gulls and terns. The Ciconiiformes were nesting in trees on two small islands in the estuary of the Newport River near Beaufort, North Carolina. Royal Terns (*Sterna maxima*), Sandwich Terns (*S. sandvicensis*), and Laughing Gulls (*Larus atricilla*) nested on Morgan Island, a dredge spoil island near the tip of Cape Lookout, North Carolina. The two terns nested together in dense colonies on sparsely vegetated or bare sand, and Laughing Gulls nested on the ground in nearby vegetation.

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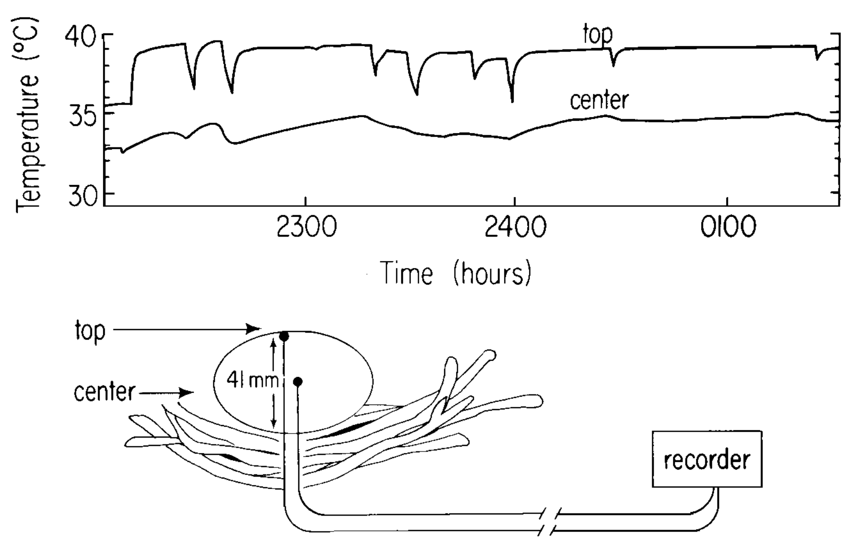

FIG. 1. Great Egret egg temperature. The top trace is the temperature at the top of the egg, adjacent to the brood patch, and the lower trace is the temperature at the center of the egg. Egg position was maintained in the nest by the thermocouples, which were threaded through the nest and run to the chart recorder.

Rates of water loss.—The change in egg mass during incubation is due almost entirely to water loss (Drent 1970). We determined rates of water loss ($\dot{M}_{H_2O}$) from naturally incubated eggs by weighing the eggs in the field at 2- to 6-day intervals with a Torbal torsion balance readable to ±0.01 g.

Physical characteristics of the egg.—The water-vapor conductance (G_{H_2O}) of eggs was measured using the method of Ar et al. (1974) in which water loss of eggs in a desiccator at constant temperature is monitored by measuring change in mass. G_{H_2O} varies with egg temperature and barometric pressure. To permit comparison with other published data we converted all our reported values to 25°C and 760 torr (101.3 kPascals) using the procedures described by Paganelli et al. (1978). The G_{H_2O} at an incubation temperature of 37°C is 1.02 times the value at 25°C.

The initial mass of eggs that were collected was measured by refilling the air cell with water at the conclusion of the experiment. For eggs that were not collected, we calculated initial mass from the egg's dimensions by the method of Hoyt (1979), using species-specific weight coefficients (K_w) determined from the collected eggs.

Egg temperature during incubation.—We measured egg temperatures with forty-gauge copper-constantan thermocouples implanted in eggs of Great Egrets (*Casmerodius albus*), Cattle Egrets (*Bulbulcus ibis*), White Ibis (*Eudocimus albus*), and Royal Terns. Two thermocouples were glued into the bird's own egg using fast-setting epoxy, one at the top of the egg and one in the center of the egg (see Fig. 1). In egret and ibis nests the thermocouple egg was placed as close as possible to the center of the 2- to 4-egg clutch, with the top thermocouple adjacent to the brood patch of the adult. The egg was anchored in place by the thermocouple leads passing through the bottom of the nest. Royal Terns usually lay a single egg, and orientation of the thermocouple egg in the nest cup was fixed by burying the thermocouple leads in the sand under the egg.

Egg temperature was recorded continuously with an Omega thermocouple D.C. millivolt amplifier and a battery-operated Linear chart recorder. We calibrated the recorder-thermocouple system before and after each series of measurements against an NBS-certified mercury thermometer. All the species studied incubated essentially continuously, so egg temperatures did not vary by more than a few degrees. The egg temperatures we report are means of temperatures taken at 30-min intervals from continuous records made during uninterrupted incubation.

Water-vapor pressure.—Water-vapor pressures in the macroenvironment around the nests (P_I) were measured in two ways. We calculated P_I from the relative humidity and temperature record of a clock-driven Serdex hygrothermograph situated about 0.5 m above the ground in the vicinity of the nests. The hygrothermograph was calibrated using saturated salt solutions (Winston and Bates 1960), and was found to be accurate within 1 torr (= 133 Pa) in the range of temperatures and relative humidities encountered. We also measured mean P_I using "egg hygrometers" (Rahn et al. 1977). These consisted of chicken eggshells of known G_{H_2O}, filled with silica gel and weighed to the nearest 0.1 mg in the laboratory before and after the period of measurement. Because the desiccant holds humidity inside the shell near

TABLE 1. Initial egg mass (M), incubation period (I), water-vapor conductance (G_{H_2O}), and rate of water loss in the nest ($\dot{M}_{H_2O}$) of 10 species of birds. F is the fractional mass loss during incubation, calculated as $F = I \cdot \dot{M}_{H_2O}/M$. ΔP_{H_2O} is the gradient in water-vapor pressure between egg and nest [$\Delta P = \dot{M}_{H_2O}\,(1.02\,G_{H_2O})^{-1}$]. Values given are means ± SD. Sample sizes, as number of eggs followed by number of clutches, are in parentheses.

	Initial egg mass (g)	I (days)	G_{H_2O} (mg · day^{-1} · torr^{-1})	$\dot{M}_{H_2O}$ (mg · day^{-1})	F	ΔP_{H_2O} (torr)
TREE NESTS						
Great Egret (*Casmerodius albus*)	48.6 ± 2.8 (26, 15)	27[a]	7.6 ± 1.2 (27, 15)	231 ± 26 (9, 4)	0.13	30
Snowy Egret (*Egretta thula*)	22.6 ± 1.5 (6, 2)	22[b]	3.8 ± 0.7 (6, 2)	121 ± 33 (9, 4)	0.12	31
Tricolored Heron (*Egretta tricolor*)	26.6 ± 1.5 (8, 4)	23[b]	3.6 ± 1.8 (8, 4)	126 ± 30 (18, 6)	0.11	35
Cattle Egret (*Bulbulcus ibis*)	27.8 ± 2.8 (19, 14)	23[a]	5.4 ± 1.5 (19, 14)	163 ± 25 (16, 10)	0.14	30 (26–31)[e]
Black-crowned Night-Heron (*Nycticorax nycticorax*)	38.8 (1, 1)	24[a]	6.2 (1, 1)	175 ± 17 (9, 4)	0.11	28
Glossy Ibis (*Plegadis falcinellus*)	37.4 ± 4.4 (6, 6)	23[a]	7.6 ± 2.0 (6, 6)	207 ± 42 (23, 7)	0.13	27
White Ibis (*Eudocimus albus*)	50.8 ± 5.7 (30, 22)	22[a]	7.8 ± 3.4 (30, 22)	290 ± 30 (18, 6)	0.13 $\bar{x}$ = 0.12	36 31
GROUND NESTS						
Laughing Gull (*Larus atricilla*)	44.6 ± 1.6 (12, 4)	23[c]	9.8 ± 2.2 (12, 4)	230 ± 41 (25, 10)	0.12	23
Royal Tern (*Sterna maxima*)	68.0 ± 5.2 (17, 17)	28[a]	13.3 ± 3.0 (17, 17)	321 ± 75 (21, 21)	0.13	24 (21–25)[e]
Sandwich Tern (*Sterna sandvicensis*)	36.1 ± 2.6 (6, 6)	25[d]	8.3 ± 1.6 (6, 6)	190 ± 40 (14, 14)	0.13	22 (21–24)[e]
					$\bar{x}$ = 0.13	23

[a] Observed incubation period, this study.
[b] Maxwell and Kale (1977).
[c] Oppenheim (1972)
[d] Langham (1974).
[e] Range of ΔP_{H_2O} given range in $\dot{M}_{H_2O}$ (Fig. 2).

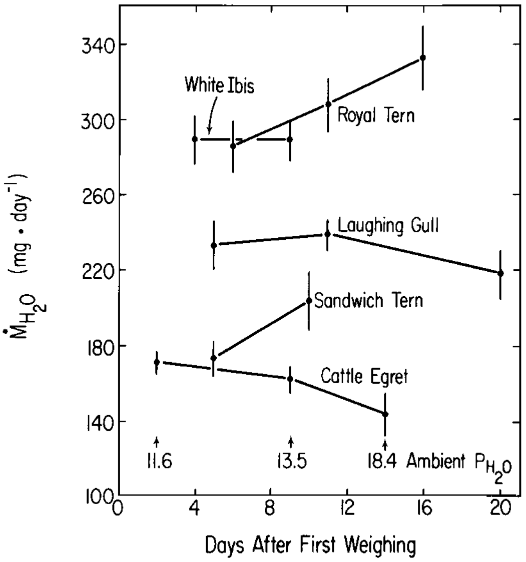

FIG. 2. Rates of water loss from eggs as a function of time. Lines connect mean values during each interval plotted at the midpoint of the interval. Vertical bars extend only ±1 standard error for clarity of presentation. Number of eggs in each group are: Royal Tern (12), Sandwich Tern (12), Cattle Egret (13), White Ibis (8), and Laughing Gull (13). Numbers under the values for Cattle Egret eggs are the mean ambient water-vapor pressures for the same interval.

zero, mean water-vapor pressure (P_{H_2O}) around such a hygrometer egg can be calculated from the equation $P_{H_2O} = \dot{M}_{H_2O}/G_{H_2O}$, where $\dot{M}_{H_2O}$ is the rate of water absorption of the egg in mg·day^{-1} and G_{H_2O} is water-vapor conductance in mg(day·torr)$^{-1}$. We placed egg hygrometers under nests of Great Egrets and White Ibis for 2–3 days to determine mean P_I and at the same time placed another egg hygrometer in the nests to determine water-vapor pressure around the eggs in the nest (P_N). The chicken-egg hygrometers differed in color and were slightly larger than the birds' own eggs, but with the exception of one Great Egret that destroyed a hygrometer, the adult birds incubated hygrometer eggs along with their own.

RESULTS

Mean daily rates of water loss varied directly with egg size, ranging from 121 mg·day^{-1} in Snowy Egret (*Egretta thula*) eggs to 321 mg·day^{-1} in Royal Tern eggs (Table 1). The $\dot{M}_{H_2O}$ of Sandwich Tern and Royal Tern eggs increased significantly (paired *t*-test, $P < 0.01$ and $P < 0.001$, respectively) from each interval to the next (Fig. 2). The $\dot{M}_{H_2O}$ of Cattle Egret eggs declined between intervals and declined significantly ($P < 0.001$) during the last interval. There was no consistent trend in $\dot{M}_{H_2O}$ of the other species. Mean values for each species are listed in Table 1.

TABLE 2. Ambient and egg temperatures measured at the center and top of the egg from two Great Egret nests and one nest of each of the other species. Numbers shown are means of temperatures taken at 30-min intervals ± SD; number of hours of observation in parentheses.

	Temperature (°C)		
		Egg	
Species	Ambient	Center	Top
Great Egret	16.7	34.3 ± 1.4 (27.5)	36.9 ± 1.6 (28.5)
Cattle Egret	21.7	36.8 ± 0.8 (44)	37.5 ± 1.1 (25)
White Ibis	20.5	—	37.1 ± 1.0 (20)
Royal Tern	24.3	37.8 ± 0.7 (13)	39.2 ± 1.2 (9.5)

The G_{H_2O} values for the various species are listed in Table 1. White Ibis eggs had an unusually wide range of G_{H_2O} values, from 3 to 15 mg(day·torr)$^{-1}$.

Mean temperature in the middle of the egg ranged from 34.3°C in Great Egret eggs to 37.8°C in Royal Tern eggs (Table 2). A significant vertical temperature gradient existed through all of the eggs measured. Temperature at the top of the egg, that part in closest contact with the brood patch of the incubating adult, averaged 1.6°C higher than at the middle. Temperatures were recorded simultaneously at the center and top of one Great Egret egg for 14 h, and a mean gradient of 4.5°C ± 1.2 ($\bar{x}$ ± SD) was found over a distance of 20.5 mm (Fig. 1).

Ambient and nest water-vapor pressures for Cattle Egret, Great Egret, White Ibis, and Royal Tern nests are shown in Table 3. Mean P_I values determined with the hygrothermograph and with egg hygrometers placed directly under heron nests over the same time interval were not significantly different ($P > 0.5$), and no distinction is made between the two methods.

The P_N values were calculated as follows. Water loss from an egg can be expressed by a form of the Fick diffusion equation as

$$\dot{M}_{H_2O} = G_{H_2O}(P_A - P_N), \qquad (1)$$

TABLE 3. Mean water-vapor pressure in eggs (P_A), in nests around eggs (P_N), and in ambient air around nests (P_I) during incubation in four species of birds. T_{egg} is estimated egg-surface temperature. See text for discussion of calculations.

				Estimated P_N (torr)		
Species	T_{egg} (°C)	P_A (torr)	$\Delta P = P_A - P_N$ (torr)	$P_A - \Delta P$	Egg hygrometer	P_I (torr)
Great Egret	35.6	44	30	14	15	12
Cattle Egret	37.2	48	30	18 (17–22)[a]	—	16
White Ibis	37.1	47	36	11	14	11
Royal Tern	38.5	51	24	27 (26–30)[a]	—	15

[a] Range of P_N given range in ΔP (Table 1).

where P_A is the water-vapor pressure in the egg and P_N is the water-vapor pressure in the nest around the egg (Rahn and Ar 1974). The term $\Delta P = (P_A - P_N)$ is the driving gradient for water loss and can be estimated as $\Delta P = \dot{M}_{H_2O}/G_{H_2O}$ (Table 1). The P_N is then equal to $(P_A - \Delta P)$ and can be calculated in two ways. First, for hygrometer eggs incubated with the natural clutch, $P_A = 0$, so $P_N = \dot{M}_{H_2O}/G_{H_2O}$. Here, $\dot{M}_{H_2O}$ is the rate of water uptake, not water loss. Second, for a natural egg, P_A approximates the water-vapor pressure at saturation at egg temperature, so $P_N = P_A - \dot{M}_{H_2O}/G_{H_2O}$. Both techniques yield similar estimates of P_N in Great Egret and White Ibis nests. We used only the second method to estimate P_N in Royal Tern and Cattle Egret nests. Because average $\dot{M}_{H_2O}$, and thus ΔP, varied over time in these two species, we calculated a range of P_N using the highest mean $\dot{M}_{H_2O}$ and the lowest mean $\dot{M}_{H_2O}$ (Table 3).

Egg-surface temperatures used to estimate P_A were assumed to be midway between temperatures recorded from the top and middle of continuously incubated eggs (Table 2), except for White Ibis eggs, for which we measured temperature at the top of the egg only. We suggest later that egg temperature, and thus P_A, may rise during incubation. If a temperature of 35°C was associated with the earliest and lowest measured $\dot{M}_{H_2O}$ and a temperature of 39°C with the latest and highest measured $\dot{M}_{H_2O}$ in the Royal Tern, then P_N would change from 21 to 28 torr over the course of incubation.

The ΔP values for each of the 10 species we studied are reported in Table 1. For the three species in which $\dot{M}_{H_2O}$ was not constant, the range in ΔP is shown. The mean ΔP for seven tree-nesting Ciconiiformes was 30.7 ± 3.3 torr ($\bar{x} \pm$ SD), whereas the mean for the three Charadriiformes was only 23.0 ± 0.6 torr. The difference between the two groups is significant ($t' = 5.95$, $P < 0.01$).

DISCUSSION

Nest humidity.—The data we present can be used to compare the microclimate around eggs in the loose stick nests of herons, egrets, and ibis with that around eggs in the ground nests of gulls and terns. Our results show that ground nests are significantly more humid than tree nests in the same macroenvironment.

The difference in ΔP between tree- and ground-nesters (Table 1) must result from differences in P_A, P_N, or both between the two classes of nests. We did not measure P_A directly, but used egg temperatures to estimate P_A values (see Results). If incubation temperatures of gull and tern eggs were 3–4°C lower than incubation temperatures of egret, ibis, and heron eggs, P_A and ΔP of the former would be reduced by enough to account for the observed difference (7.7 torr) in ΔP. This is not the case, however. The average temperature of a Royal Tern egg was actually higher than temperatures of Great Egret, Cattle Egret, or White Ibis eggs (Table 2). For seven species of gulls and terns for which egg temperatures have been reported (Howell and Bartholomew 1962, Drent 1970, Morgan et al. 1978, Rahn and Dawson 1979, Pettit et al. 1981), average egg temperatures are in no case lower than those we measured in egrets and ibis.

We conclude that the difference between ΔP values for the two groups must be due to a difference in P_N. That is, the ground nests of gulls and terns are more humid than tree nests of herons, egrets, and ibis in the same macroenvironment. In four species, we have the data necessary to estimate P_N itself, and not just ΔP (Table 3). The estimated mean P_N around a Royal Tern egg is 9–16 torr higher than that around Great Egret, Cattle Egret, or White Ibis eggs.

High P_N in ground-nesters initially seems surprising. To the human observer the bare open sand on which the terns nest is a more desiccating environment than are the often shaded nest sites of herons. Both groups of birds incubate nearly continuously, so differences in parental attentiveness are unlikely to account for the differences in P_N. Rather, the likely explanation for the observed difference can be found from a consideration of the sources of water vapor in a nest and the avenues for water loss from the nest. Tree-nesting herons build loose stick nests that do not present much of a barrier to convective and/or diffusive gas exchange. Water vapor added to the nest from the egg or incubating adult is quickly lost to the ambient air. When ambient conditions are similar, ground nests have higher P_N than tree nests for three reasons: (1) the ground itself is an important source of water vapor (Geiger 1965), (2) the relatively solid surface of the ground reduces water loss from the nest by convection and diffusion, and (3) wind speed on the ground is less because nests are in the boundary layer. The P_N of the Great Egret and White Ibis nests measured with egg hygrometers was only 0–3 torr higher than water-vapor pressure in the macroenvironment (P_I), while the calculated mean P_N in the Royal Tern nests was 12 torr higher than water-vapor pressure in the macroenvironment (Table 3).

Our data provide direct evidence that nest site and structure can have a significant effect on the gradient in water-vapor pressure between the nest and the macroenvironment. Data compiled by Walsberg (1980) provide an independent test of this hypothesis. In 10 ground-nesting species the mean gradient of water-vapor pressure between nest and ambient conditions ($P_I - P_N$) was 8.2 ± 4.3 torr ($\bar{x}$ ± SD). For two tree-nesting species (*Anous tenuirostris* and *Gygis alba*) the mean gradients were 3 and 0 torr, respectively. Despite differences among investigators, their techniques, and the habitats in which they worked, the difference in $P_I - P_N$ between ground nesters and tree nesters is marginally significant (Mann-Whitney $U = 19$, $P = 0.1$). If we include data from the four species reported here, the difference becomes highly significant ($P < 0.01$).

Egg water-vapor conductance.—Nest humidity is of physiological significance to a developing embryo, because it affects $\dot{M}_{H_2O}$ and the hydration state of that embryo, but $\dot{M}_{H_2O}$ depends on G_{H_2O} as well as on ΔP. In order to compare G_{H_2O} values between different species, it is necessary to take the effects of egg size and incubation period into account. Hoyt (1980) presented an equation that expresses the interrelation between these parameters for 143 species of birds:

$$G_{H_2O} = 2.32\ (M^{0.976}/I^{0.73}), \qquad (2)$$

where M is initial egg mass in g and I is incubation period in days. If our measured G_{H_2O} values are expressed as a percentage of the value predicted for eggs of the same M and I from equation 2, G_{H_2O} averages 78 ± 11% ($\bar{x}$ ± SD) of the predicted values for 7 tree-nesters and 107 ± 6% for 3 ground-nesters. These two percentages are significantly different ($t' = 5.36$, $P < 0.01$). That is, eggs laid in stick nests in trees, which are incubated in less humid microenvironments, have relatively lower G_{H_2O} than eggs of ground nesters, which are incubated in more humid microenvironments. Lomholt (1976) and Birchard and Kilgore (1980) reported a similar relationship between G_{H_2O} and nest humidity in several other species of birds.

Because G_{H_2O} is high in ground-nesting species, where ΔP is low, and low in tree-nesting species, where ΔP is high, the total water loss during incubation, expressed as a fraction of initial mass (F), is not significantly different between the two groups (Table 1, $t = 0.44$, $P > 0.5$). Estimates of F depend on $\dot{M}_{H_2O}$, which is not always constant (see below). The measurements of $\dot{M}_{H_2O}$ that we used to estimate F extended over 45–90% of the incubation period for each species, however, so it is unlikely that $\dot{M}_{H_2O}$ could vary enough during the remainder of the incubation to change the conclusions above.

Changes in rates of water loss from eggs.—In the Royal Tern, Sandwich Tern, and Cattle Egret daily rates of water loss during natural incubation changed with time (Fig. 2). Because few studies of egg water loss have been carried out over the whole incubation period, it has generally been assumed that $\dot{M}_{H_2O}$ remains constant. Drent (1970), however, showed that the $\dot{M}_{H_2O}$ increased during the early stages of incubation in the Herring Gull (*Larus argentatus*), and $\dot{M}_{H_2O}$ of eggs of four other gulls also varies over time (Morgan et al. 1978, Rahn and Dawson 1979). Change in rate of water loss from an egg can result from one or more of the following: (1) change in G_{H_2O}; (2) change in nest humidity, P_N; or (3) change in P_A, due to change in surface temperature of the egg.

Water-vapor conductance of eggs increases during the first few days of incubation in several species of passerines but is relatively constant after the development of the chorioallantois (Carey 1979, Hanka et al. 1979, Birchard and Kilgore 1980, Sotherland et al. 1980). Most of our measurements of G_{H_2O} were made using eggs that had been incubated at least 10 days (the same eggs in which we measured $\dot{M}_{H_2O}$). Exceptions were the Laughing Gull eggs, which were all freshly laid, and some White Ibis eggs. We could detect no significant change in G_{H_2O} of White Ibis eggs during development ($t = 0.98$, $P > 0.2$). The G_{H_2O} of 12 freshly laid eggs was 8.59 ± 2.20 mg(day·torr)$^{-1}$ ($\bar{x} \pm$ SD), and the G_{H_2O} of 13 eggs containing well-developed embryos was 7.00 ± 2.49 mg(day·torr)$^{-1}$. It may be that G_{H_2O} increases with development of the chorioallantois only in small (<10 g) eggs, as Birchard and Kilgore (1980) suggested. Even if G_{H_2O} changes early in incubation, such changes cannot account for the variations in $\dot{M}_{H_2O}$ of Royal Tern and Cattle Egret eggs very late in incubation.

In the absence of any evidence that G_{H_2O} changes during middle to late incubation, these changes in $\dot{M}_{H_2O}$ are presumably due to changes in nest humidity, egg temperature (and hence P_A) or both. Our measurements of egg temperatures and nest humidities did not extend over the entire period of $\dot{M}_{H_2O}$ measurements, so we cannot be certain of what caused the observed changes in $\dot{M}_{H_2O}$. The available data, however, suggest that changes in P_N may be sufficient to account for the variation in $\dot{M}_{H_2O}$ in Cattle Egret eggs, but not in the two tern species.

For 7 of the 10 species in which we measured $\dot{M}_{H_2O}$, neither $\dot{M}_{H_2O}$ nor ambient humidity changed significantly during the period of measurement. The gradual decline in $\dot{M}_{H_2O}$ of Cattle Egret eggs, however, was correlated with a gradual increase in P_I, the average humidity in the macroenvironment (Fig. 2). The close correlation between P_N and P_I in ciconiiform nests (Table 3) suggests that P_N might have increased by an equivalent amount, about 7 torr. All other things being equal, this would reduce ΔP, the gradient driving water loss from the egg, and therefore reduce $\dot{M}_{H_2O}$ (see equation 1). The predicted reduction in $\dot{M}_{H_2O}$ closely approximates the observed changes.

The observed increases of 20% and 17% in $\dot{M}_{H_2O}$ in Sandwich and Royal terns, respectively (Fig. 2), cannot adequately be accounted for by changes in P_I. At least part of the increased rate of water loss may be due to an increase in surface temperature of the egg. Drent (1970) found that temperature in the nest of the Herring Gull and in the center of the egg rose steadily during the first two-thirds of incubation. In addition, heat production of the developing embryo late in incubation is sufficient to raise egg-surface temperature in some species (Drent 1970, Vleck unpubl.). Even at a constant nest humidity, the observed 17% increase in $\dot{M}_{H_2O}$ in Royal Tern eggs could be accounted for by only a 1.3°C rise in mean surface temperature of the egg. A complete understanding of the causes of variation in $\dot{M}_{H_2O}$ will require measurement of G_{H_2O}, P_N, and egg temperature throughout the incubation period.

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HUNTING BEHAVIOR, PREY SELECTION, AND ENERGETICS OF SNAIL KITES IN GUYANA: CONSUMER CHOICE BY A SPECIALIST

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ABSTRACT.—The hunting behavior, snail size selection, and time-activity patterns of nonbreeding Snail Kites (*Rostrhamus sociabilis sociabilis*) were studied in Guyana rice fields. Kites spent 62% of the photoperiod perching, 19% foraging, 13% in maintenance activities, and 6% flying. As the day progressed, the percentage of daylight hours spent perching increased significantly, while foraging decreased significantly. Kites successfully captured and ingested *Pomacea* snails in 78% of the foraging bouts observed. The mode of hunting was evenly split between coursing (50.7%) and still-hunting (49.3%). Searching and returning times were related to time of day, as significantly more coursing hunts and still-hunts occurred in mornings and late afternoons, respectively. Prey handling time was the most time-consuming component of a foraging bout. Time spent searching for prey, returning, or handling prey was not related to snail size. The size distribution of captured snails differed significantly from that of available snails; kites selected more medium snails and fewer small snails and took large snails in equal frequency to that at which large snails were available. Kites captured the same-sized snails when coursing as when still-hunting. As rice grew, kite utilization of rice fields declined, and the frequency of still-hunting decreased while course-hunting attempts increased. The daily caloric intake of kites was estimated to be 104.2 kcal, the daily energy expenditure 85.7 kcal. Results are discussed in relation to consumer choices of specialists. The most important decision a foraging Snail Kite may make is what patch to search in and how long to search before abandoning patches. *Received 14 January 1982, accepted 28 June 1982.*

LITTLE is known about the hunting behavior and foraging ecology of the Snail Kite (*Rostrhamus sociabilis*). Long recognized as an extreme diet specialist, the Snail Kite feeds almost exclusively on *Pomacea* snails (Haverschmidt 1962, Snyder and Snyder 1969, Voous and van Dijk 1973; for exceptions see Sykes and Kale 1974, Beissinger in prep.). A kite captures a snail by flying over a marsh, extending a foot, and grabbing the mollusc with long toes near the water surface. It then perches in order to extract the body from the shell with its thin, sharply hooked bill. Two modes of hunting have been observed (Snyder and Snyder 1969, Haverschmidt 1970): "still-hunting" kites visually search from a perch and capture a snail near that perch after a short flight; "course-hunting" kites fly 3–5 m above a marsh, usually facing into the wind, visually searching until a capture occurs. Snyder and Snyder (1969) and Voous and van Dijk (1973) described in detail how kites extract and consume snails, but there is no quantitative information on the behavior and energetics of kite foraging. In this paper, I describe the foraging ecology of the Snail Kite (*R. s. sociabilis*) on the basis of field observations of hunting behavior, activity patterns, and prey selection in rice fields in Guyana, South America.

STUDY AREA AND METHODS

Studies were conducted from July–August 1977 at the Rice Research Station and surrounding rice fields on the coastal lowlands (1.4 m below sea level) at the Mahaicony and Arbary Rice Development Scheme (MARDS), Burma, Guyana, South America (6°28′N, 57°45′W). The freshwater marshes or mangroves that once covered this region have been almost totally replaced by rice cultivation (6,721 ha in 1976; Kennard pers. comm.), with few fields remaining fallow. There are two rainy and two dry seasons (Cummings 1965). Rainfall during the study period totaled 14.76 cm in July, the end of the long rainy season, and 3.84 cm in August, the onset of the short dry season. Daily minimum and maximum temperatures ranged from 22–31°C. For a more detailed description of the study area, see Giglioli (1959), Osborne and Bourne (1977) and Bourne and Osborne (1978).

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A 26-ha study site of seven fields was selected for behavioral observations of kites. Strip censuses of Snail Kites and Limpkins (*Aramus guarauna*) were made one to five times weekly from 0700 to 0800. Fieldwork was initiated near the time of sowing. Rice had reached full height by the end of the study 6–8 weeks before harvest.

I marked 14 fence posts on the border between two fields and cleared the surrounding area of old snail shells so that I could sample the size of snails selected by kites. As many as 14 kites were observed foraging from these posts during strip censuses but four was the average. Posts were selected because of easy accessibility and use by foraging kites. Fence posts ranged from 7 to 17 cm in diameter and 1 to 1.5 m high. Empty snail shells were collected from beneath each post on 14 occasions with periods of 24–48 h between collections. Aperture length was measured to the nearest millimeter, and after one week three size classes were delineated: small (11–24 mm), medium (24–28 mm), and large (29–36 mm).

I attempted to estimate the relative abundance of the three size classes of snails in the two fields from late July through early August. Because water turbidity was great, I could not detect snails visually. I collected snails by walking or crawling a transect through the field, tactilely searching the mud and plant surfaces with both hands. A total of 20 h was spent sampling snails in kite feeding areas. Thirty-four of these snails (13 large, 9 medium, and 12 small) were collected for caloric analyses. After extraction from the shell, albumen glands were discarded (as kites do not generally ingest them; see Snyder and Snyder 1969), and each snail was oven dried for 28 h at 100°C, when dry weight became constant. Ten snails were individually ground in a Wiley Mill, and caloric determinations were made on 40-mg samples of each through use of a Phillipson Microbomb calorimeter.

I monitored Snail Kite activities by observing focal individuals (Altmann 1974) chosen at random for 15-min periods from 20 to 75 m away through spotting scope and binoculars. As there was no breeding colony of kites in the vicinity and kites that were observed extracted and ate snails in the study area, none of the focal individuals was assumed to be breeding during the time of the study. Activities were recorded directly into a tape recorder and later timed to the nearest second with a stop watch. Three time periods were chosen a priori to homogenize air temperature trends within periods (morning: from sunrise at 0630 to 1100; midday: from 1100 to 1500; and late afternoon; from 1500 to 1830, just before sunset). A total of 60 focal samples was distributed almost evenly throughout the daylight hours (morning 19, midday 21, late afternoon 20). I tried not to sample the same kite more than once a day by sampling during only one time period a day.

Activities were categorized as follows. (1) Perched birds were sitting upon a fence post, vegetation, or mudflat. It was not possible to determine reliably whether perched birds were engaged in searching activities (i.e. still-hunting), and no attempt was made to separate perched birds into those searching or those not searching for snails. Thus, still-hunting kites visually searching for prey while perched were included in this category. (2) Maintenance activities included preening, scratching, feather ruffling, wing stretching, wing drying, and bill cleaning. (3) Flying was defined as movements for the purpose of changing location of perches or hunting areas, as well as flights to or from roosting areas. (4) Aggression was observed mainly in the form of the supplanting of one individual by another or by active chasing of another kite. Finally, (5) foraging included all activities associated with the capture and ingestion of snails. A foraging bout was composed of searching (flight in the pursuit and capture of snails, including both coursing and still-hunting), returning (flight from the point of capture to any perch where the prey was consumed), and handling (the extraction of a snail from its shell and ingestion). The time between foraging bouts ("between") was calculated as the amount of time that elapsed between ingestion of a snail and the initiation of the next searching flight. For each capture clearly observed (79% of the captures), I visually estimated the snail size class. From experience gained while measuring over 1,000 snail shells, I usually was able to estimate the aperture length within 1 mm. A comparison of my estimate of the distribution of snail size classes that kites fed upon during periods of behavioral observation and the distribution of snails collected beneath feeding perches revealed no significant difference ($\chi^2 = 0.94$, df = 2, $0.50 < P < 0.70$). This supported my ability to assign captured snails correctly to the three size classes.

Statistical analyses were conducted using parametric procedures on the Statistical Analyses System (S.A.S.) at Miami University and Wayne State University. Assumptions of normality and homoscedasticity of parametric models were tested by inspecting scatter and residual plots, skewness and kurtosis coefficients, and comparing sample variances. Nonparametric statistics were used when assumptions were violated. Because percentage data were not normally distributed and often outside the 30–70% interval, they were arcsine transformed before analyses. Differences were designated as significant if $P < 0.05$.

RESULTS AND DISCUSSION

Daily activity.—Snail Kites usually arrived individually at foraging stations, presumably from a communal roost to the north, between dawn (0630) and 1100, with occasional arrivals or departures during the course of the day.

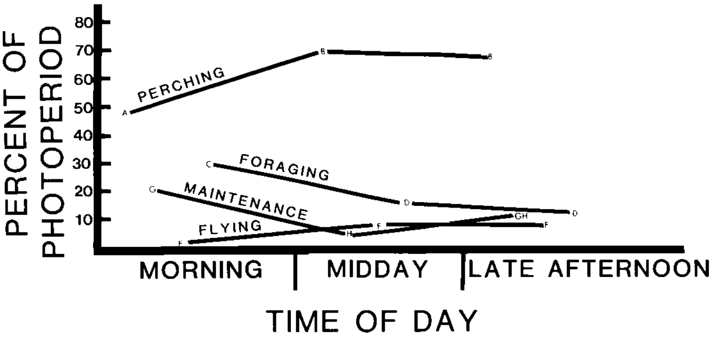

Fig. 1. The activity pattern of Snail Kites in Guyana rice fields relative to time of day. Different letters within activity types indicate significant differences between time period means as tested by Duncan's Multiple Range test.

Twice, I observed group movements away from the study area during the day. It appeared, however, that most of the individuals foraging in the area remained there for the entire day until departing for the roost again 0.5–1 h before sunset. Although kites were not individually marked, certain fence posts were consistently occupied during some periods of the study, perhaps by the same individual.

The diurnal activity pattern of Snail Kites is presented in Fig. 1. Kites spent the majority of the daylight hours perching (62%), followed by foraging (19%), maintenance (13%), and flying (6%). Less than 0.1% of the photoperiod was spent in aggressive behavior, which was observed only twice during the 60 sampling periods. Although aggression associated with feeding territories has been occasionally observed in Florida (Snyder and Snyder 1970), I saw no evidence of this in Guyana. Because aggressive behavior was a minor proportion of Snail Kite activities, it was excluded from the remainder of the analyses in this paper.

Activity patterns changed with time of day: the percentage of photoperiod spent perching increased significantly from morning to midday and late afternoon, while foraging decreased significantly during this time (Fig. 1). As it was not possible to determine reliably whether a perched kite was searching visually for prey (still-hunting) or simply resting, all perched kites were assumed to be resting, which resulted in lower foraging and increased resting values. This bias does not apply to energy budgets constructed later from these data, however, as the energetic cost of perching and perching while visually searching are nearly identical (King 1974).

Despite fluctuations during the day in the amount of time spent in maintenance and flying activities, no statistically significant trends were noted (Fig. 1). Maintenance was highest in the morning, most likely in response to frequent morning rainstorms. Morning values for flying were lowest but would have been higher if flights from the roost to the foraging grounds could have been observed.

Hunting behavior.—I observed 74 foraging bouts by kites, and 82% of these were successful. All food items were *Pomacea* snails. In only 78% of the bouts was the snail completely ingested, however, as kites dropped snails three times during the process of handling them on a perch. On one of these occasions, a young-of-the-year kite (identified by plumage characteristics; Haverschmidt 1968) had difficulty perching with the snail in its talons, a behavior often seen in young kites in Florida (pers. obs.). I do not know in the other two cases whether the snails were rejected purposely (e.g. a capture of an empty shell) or dropped accidently. In summary, Snail Kite predatory efficiency was similiar to the mean value of 73% that Collopy (MS) noted for other invertebrate-eating birds, the most successful avian predators, but much higher than he found for fish-eaters (45%) and those hunting primarily mammals (27%) or birds (8%). When snails were available, kites had little trouble capturing them.

Both hunting modes were equally employed by kites: 50.7% of the foraging bouts observed were coursing hunts and 49.3% were still-

TABLE 1. Descriptive statistics for the components of a Snail Kite foraging bout.

Foraging components	Number of observations	$\bar{x}$ ± SD (s)	Range (s)	$\bar{x}$% ± SD (s) of complete bouts
Coursing				
Searching	36	88 ± 69	16–303	44 ± 13
Returning	28	17 ± 15	1–79	11 ± 8
Handling	27	73 ± 27	32–150	45 ± 12
Still-hunting				
Searching	35	4 ± 4	1–13	5 ± 5
Returning	30	4 ± 3	1–12	7 ± 5
Handling	33	66 ± 34	21–200	88 ± 7
All hunts				
Searching	71	47 ± 64	1–303	24 ± 21
Returning	58	11 ± 12	1–79	9 ± 7
Handling	60	69 ± 31	21–200	67 ± 23
Between	43	146 ± 172	10–710	—

hunts. In Florida, young kites have been observed to still-hunt, but adults rarely do so except in times of food stress during regional drought, when kites are forced to forage along woody lake margins or along canals (Snyder and Snyder 1969, Beissinger in prep.). Snyder and Snyder (1969) attribute the high incidence of still-hunting by kites in Guyana to the availability of more suitable perches along rice fields and canals. The hunting success of both methods was similar, as 81% of 36 coursing-hunt attempts and 83% of 35 still-hunt attempts were successful.

Descriptive statistics associated with the components of a Snail Kite foraging bout are summarized in Table 1. The mean searching time for coursing hunts was 22 times more than for still-hunts, but this was partly due to the manner in which these parameters were measured, concealing still-hunt searching time within perching time and thus disproportionally lowering searching times for still-hunts. In comparison to the other components of a foraging bout, prey handling was the most time consuming. For all hunts, handling constituted an average of nearly 68% of a bout. Even the handling time for coursing hunts (45.2%), which may be the most meaningful value because searching time is totally measured, indicated that handling a snail is as time consuming as finding one.

The amount of time spent searching and returning by kites was related to the time of day (Table 2). When observations of both hunting modes were pooled, mean searching and returning times decreased significantly throughout the day. Searching times for coursing hunts showed a similar but not significant trend. Decreased search times probably were related primarily to the proportion of still-hunts and coursing hunts that occurred in the three time periods: 58% of the coursing hunts occurred in the morning, while 46% of the still-hunts occurred in the late afternoon (from Table 2). The distributions of still-hunts and coursing hunts throughout the three time periods were significantly different ($\chi^2 = 9.38$, df = 2, $P < 0.01$). Three explanations could account for this shift in foraging mode: (1) as ambient air temperature increased during the day, the costly exertion of long coursing flight was avoided because the energetic requirements for flight increase proportionally with increases in ambient air temperature (Kendeigh et al. 1977); (2) by coursing in the morning, Snail Kites may have been investing time exploring the prey base of the chosen foraging patch, a tactic reported for other avian predators (Smith and Sweatmen 1974, Davies 1977); and/or (3) with increasing water temperature, snails become more active (McClary 1964) and inspire near the water surface more often, increasing the encounter rate (and still-hunting success) for perching kites. Neither handling time nor time between captures (a measure of feeding rate) showed any significant trends in relation to time of day (Table 2).

No significant differences were found in the amount of time required for foraging-bout components in relation to snail size (Table 3).

TABLE 2. Variation in the components of a Snail Kite foraging bout during three time periods.

	Mean ± SE (*n*) s by time of day			
Foraging component	Morning	Midday	Late afternoon	p[a]
Coursing				
Searching	95 ± 16 (21)	94 ± 27 (8)	60 ± 14 (7)	0.628
Returning	17 ± 2 (20)	24 ± 14 (5)	8 ± 4 (3)	0.245
Handling	69 ± 5 (19)	70 ± 11 (5)	101 ± 25 (3)	0.462
Still-hunting				
Searching	4 ± 2 (9)	6 ± 1 (11)	2 ± 1 (15)	0.107
Returning	4 ± 1 (8)	6 ± 1 (9)	4 ± 1 (13)	0.282
Handling	57 ± 4 (10)	90 ± 19 (9)	58 ± 5 (14)	0.708
All hunts				
Searching	68 ± 14 (30)	43 ± 15 (19)	21 ± 7 (22)	0.020
Returning	13 ± 2 (28)	12 ± 5 (14)	4 ± 1 (16)	0.003
Handling	65 ± 4 (29)	83 ± 13 (14)	65 ± 7 (17)	0.734
Between	122 ± 66 (21)	160 ± 55 (10)	175 ± 66 (12)	0.448

[a] Significance levels based on Kruskal-Wallis test (Chi-square approximation).

Searching and returning times decreased relative to snail size, but this was not statistically significant. The trend of decreased search times for larger snails seems to run counter to the potential encounter rate, which would be lower for the less common, larger snails (Fig. 2). The possibility that kites foraged by searching for larger snails but took smaller snails after a time without capture in order at least to stay even with energy expenditures might account for the shorter searching times observed for less common, larger snails. For all hunts, handling time was very consistent, with a mean for the three size classes of 67 s. Because the cost in time (and presumably energy) required to find a snail, return to a perch, and extract and ingest the snail did not differ significantly for snails of different sizes, the profitability of a snail can be defined merely by its total energetic value (Krebs 1978, Schoener 1979).

An interaction between time of day and snail size might have been responsible for the outcome of the above results. Despite not meeting the assumption of normality, a two-way analysis of variance (ANOVA) model was constructed to test for interaction. One-way ANOVA models were examined simultaneously with the Kruskal-Wallis tests previously re-

TABLE 3. Variation in the components of a Snail Kite foraging bout in relation to the size class of snail captured.

	Mean ± SE (*n*) s for snail size			
Foraging component	Small	Medium	Large	p[a]
Coursing				
Searching	78 ± 15 (8)	54 ± 9 (10)	53 ± 21 (2)	0.402
Returning	15 ± 3 (8)	17 ± 3 (10)	7 ± 2 (2)	0.336
Handling	60 ± 6 (8)	65 ± 11 (10)	93 ± 6 (2)	0.168
Still-hunting				
Searching	6 ± 2 (8)	3 ± 1 (9)	3 ± 1 (6)	0.245
Returning	6 ± 1 (8)	4 ± 1 (9)	4 ± 1 (6)	0.507
Handling	72 ± 16 (10)	71 ± 9 (10)	58 ± 4 (6)	0.440
All hunts				
Searching	42 ± 12 (16)	30 ± 8 (19)	16 ± 9 (8)	0.340
Returning	10 ± 2 (16)	11 ± 2 (19)	4 ± 1 (8)	0.200
Handling	66 ± 9 (18)	68 ± 7 (20)	67 ± 6 (8)	0.604
Between	131 ± 51 (10)	145 ± 52 (12)	259 ± 119 (6)	0.444

[a] Significance levels based on Kruskal-Wallis test (Chi-square approximation).

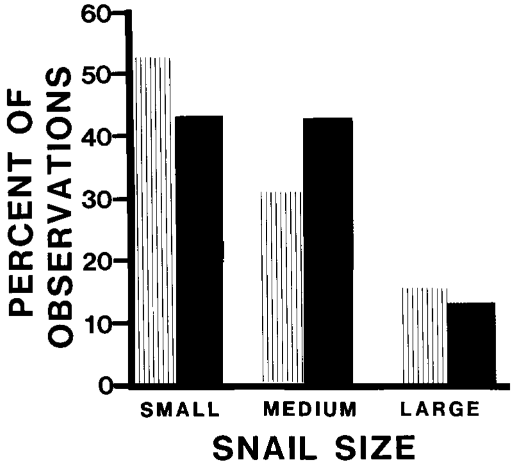

Fig. 2. The sizes of *Pomacea dolioides* potentially available (striped bars) to Snail Kites and sizes taken (dark bars).

ported (Tables 2, 3), and in all cases parametric and nonparametric tests yielded similar values. From the two-way ANOVA model, there was no evidence that a time of day and snail size interaction occurred for searching ($F = 0.70$, $P = 0.596$) or returning times ($F = 0.07$, $P = 0.991$).

Snail size selection.—I collected 959 *Pomacea* shells that had been eaten by kites. Over 99% of the snails were *Pomacea dolioides*; *P. glauca* composed the remainder of the sample. Snyder and Snyder (1969) also noted Snail Kites in Guyana feeding heavily on *P. dolioides* near the water surface and rarely upon *P. glauca*, a less abundant and more aquatic bottom dweller.

From transect searches, I collected 155 *P. dolioides* to serve as a sample of the size distribution of snails potentially available to kites. Figure 2 compares the sizes of snails available and those chosen by kites. There was a significant difference between the frequency of size classes available to kites and those selected ($\chi^2 = 7.632$, df = 2, $P = 0.022$). It appears that Snail Kites avoided the more abundant small snails, preferred the medium sized snails, and took the large snails in approximately equal frequency with those that were available.

Because snails are captured by kites on the wing, snail availability is a function of: (1) snail density; (2) snail depth below the water surface; (3) the effects of water temperature and dissolved oxygen on *Pomacea* inspiratory and surfacing behavior (McClary 1964, Freiburg and Hazelwood, 1977); and (4) the density of vegetation covering the water surface. I sampled snail availability in a manner that assumed that factors affecting availability act similarly on all sizes of snails. If not, then the size distribution of snails that was collected from the field might not be the same as that available to kites. For instance, large snails may be less vulnerable to predation, because they may have respiratory rates that are less affected by changing water temperatures, causing them to surface less often, or they may frequent dense vegetation more often than small snails.

The choice of snail size could be affected by one other factor—snail parasite loads. Grossman and Hamlet (1964) state that kites are infected by "lung flukes" carried by *Pomacea* snails but offer no direct evidence of parasitism or references. At least eight trematode species are described from *Pomacea* snails, and birds are definitive hosts in all three cases where life histories are known (Nasir and Rodriguez 1969; Nasir et al. 1969a, b; Nasir and Silva 1972; Gascon 1975; Hanning and Leedom 1978). Gigantism, increased shell thickness, and shell abnormalities in molluscs sometimes result from parasitism (Cheng 1971, Hanning 1978) and might offer kites a mechanism to reject highly parasitized individuals. Because parasitic loads do increase with snail size in *Pomacea paludosa* (Hanning 1978), kites may not have taken large snails more often in order to avoid higher infection rates.

Coursing hunts require far more flying, a very energetically expensive activity (Table 4), than do still-hunts. Course-hunting Snail Kites would be expected to choose larger snails in order to gain a greater energetic payoff to offset increased costs (Schoener 1969, 1979), especially as searching time is unrelated to snail size. No differences in the distributions of snail size classes selected by coursing or still-hunting kites occurred when all three size classes were considered ($\chi^2 = 1.85$, df = 2, $0.60 < P < 0.70$) or when medium and large size classes were combined and tested against small ($\chi^2 > 0.750$, df = 1, $P > 0.750$).

Effects of rice growth.—Figure 3 illustrates the declining use of rice fields by Snail Kites during the study period. When rice fields were drained, kite numbers were highest. As irrigation and rice growth commenced, kite use significantly declined, until no birds were observed in mid-August. A highly significant

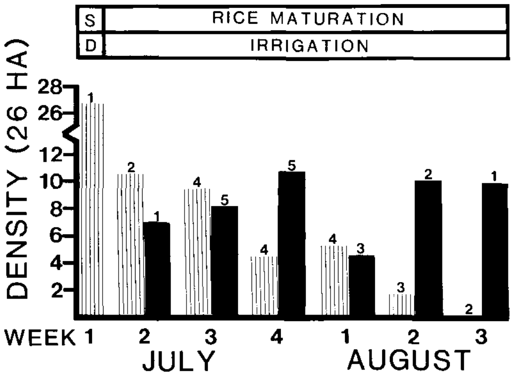

Fig. 3. Weekly mean density of Snail Kites (striped bars) and Limpkins (dark bars) determined by strip censuses in Guyana rice fields. The number of weekly counts appears above each bar. Upper horizontal bars indicate the duration of sowing (S), rice growth and maturation, drainage (D), and irrigation.

TABLE 4. A simplified energy budget for nonbreeding Snail Kites. Equation 10 from Koplin et al. (1980) was used to calculate energy cost, assuming an average daily air temperature of 27°C (pers. obs.) and a mean body weight of 367.6 g, the mean of seven observations from Haverschmidt (1968, 1970), and specimens from the Museum of Zoology, University of Michigan.

Activity	Proportion of 24-h day	Energy cost (kcal)
Nonflight	0.945	59.1
Flight	0.055	26.6
Total	1.000	85.7

(P = 0.002, r^2 = 0.747, n = 20) linear correlation between daily counts and week was found for Snail Kites but not for Limpkins (P = 0.620, r^2 = 0.125, n = 18). As rice grows, foraging becomes more difficult for kites because: (1) the area of water surface that a kite can visually scan while hunting decreases and (2) to make a capture, a kite's descent to the water must be unhindered by vegetation. For effective foraging, Snail Kites need sizeable patches of open water with floating but not tall emergent vegetation. Limpkins are able to search tactilely for *Pomacea* snails while wading (Snyder and Snyder 1969) and can forage successfully in heavily vegetated areas. In the study area, they utilized fallow fields until rice reached approximately a 0.5-m height.

Assuming relatively stable snail populations, snail availability should decrease as rice grows, and the encounter rate of still-hunting kites should decrease. In response, Snail Kites should course-hunt more often to increase encounter rates by searching a greater area. To test this, I examined the proportion of still-hunts that occurred during the first 2 weeks of behavioral observations, when rice was absent or low, and the last 3 weeks, when rice was highly emergent. Because hunting mode was related to time of day, I used only the 24 hunts that occurred in the late afternoon, when still-hunting was most frequent for this analysis. The proportion of coursing hunts increased significantly (χ^2 = 5.93, df = 1, $P < 0.025$) from 0% (n = 9) in the first 2 weeks to 47% (n = 15) in the last 3 weeks. These results are opposed to predictions from models by Norberg (1977) that predators should employ less energy-consuming hunting methods as prey density decreases.

Energy budget.—The daily food intake of Snail Kites was calculated by proportionately reducing the distribution of the three size classes for the 68 snails consumed during the 15 h of time-activity observations to that which would have occurred in a 12-h Guyana photoperiod. Caloric values per gram dry weight for *P. dolioides* were relatively constant ($\bar{x} \pm$ SD = 4.04 ± 0.09, n = 10). Using mean dry weights for each snail size class and assuming an assimilation efficiency of 0.9, a value chosen because snail tissue is almost entirely digestable and raptor assimilation efficiencies peak near this value (Sarker and Naulleau 1981), I calculated the daily energy intake by Snail Kites to be 104.2 kcal.

An average daily energy expenditure for Snail Kites was calculated in the following manner. As kites spent 12 h a day roosting, means from the 60 time-activity samples (Fig. 1) were pooled to determine the mean percentage of each daily activity for a 24-h period. Because Snail Kites spent less than 20% of the photoperiod in flight activities, equation 10 from Koplin et al. (1980) was used to compute the daily energy budget (Table 4). Daily energy expenditure for Snail Kites was estimated to be 85.7 kcal (Table 4).

My calculations indicate that kites easily utilized rice fields to meet their daily energy needs, realizing a daily net energy gain of 18.5 kcal. The high proportion of snails captured by energetically inexpensive still-hunting probably accounted for this large net energy gain. During the study period, I saw no evidence that kites were ever stressed to find food or that any were malnourished. On the contrary, the small proportion of time spent flying by kites in rice fields (Table 4) may indicate that this was a very profitable patch to exploit.

Consumer choice by a specialist.—Snail Kites are a classic example of a "specialist." Preying almost solely on one genus of freshwater snails (often one species in some portions of its range), kites need not distinguish among a number of different items to be included in the diet. Under most conditions a kite may need only to choose among food items by size as it relates to the energetic benefit of caloric intake and the energetic cost of searching and handling times.

In this study, no increased cost was associated with the pursuit, capture, handling, and ingestion of prey in relation to prey size. No additional energetic benefit in terms of calories per capture was accrued during costly coursing hunts as compared to still-hunts. Snail Kites avoided capture of smaller snails, selectively preyed on medium-sized ones, and did not take large snails more frequently than they were encountered. In addition, patch use and hunting mode were affected by rice growth. Rice fields proved to be an easy place for kites to meet their energetic needs.

MacArthur (1972) partitioned the process of food gathering into four phases: (1) where to search; (2) how to search and what to look for; (3) whether to pursue or ignore a food item; and (4) the capture attempt and ingestion. Kite morphology is so specialized (Snyder and Snyder 1969) that, in order to maximize snail capture and ingestion proficiency (4), the decision of what foods to search for (2) has already been determined. A Snail Kite need only decide on where to search (1), how to search (2), and (3) whether or not to include an item in its diet on the basis of size. These decisions may be based on the encounter rate within a given patch.

In the choice of hunting modes, kites might be expected to still-hunt exclusively if they could find enough food. When insufficient numbers of snails per unit time are available from a perch, kites should shift to coursing. Thus, the effectiveness of still-hunting may be primarily controlled by the snail-encounter rate within the patch as a function of the distance from the still-hunting perch. Factors that affect snail-encounter rates can cause a shift in hunting mode: the vegetative structure of a patch may be a prime determinant, as still-hunting increased with rice growth during the 2 months of study, and environmental factors (e.g. air and water temperature, dissolved oxygen, and wind speed) that affect both snail-encounter rates and kite metabolic costs probably accounted for the diurnal shift by kites in the mode of hunting that was observed.

Because Snail Kites selectively avoid small snails, a kite might be expected to prefer large snails. The diet should vary from patch to patch, however, depending upon the distribution of size classes available and the energetic costs of capture, which are both functions of the encounter rate and hence of patch choice. Patches do vary greatly in snail density and size distribution (Bourne and Berlin 1982). Thus, the most important decision a foraging Snail Kite must make is what patch to search in and how long to search before abandoning one patch for another.

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MOLLUSK PREDATION BY SNAIL KITES IN COLOMBIA

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ABSTRACT—Snail Kites (*Rostrhamus sociabilis sociabilis*) observed along the lower Río Magdalena in northern Colombia fed heavily on *Pomacea chemnitzi* but also took *Marisa cornuarietis*, a smaller species. The kites captured *Pomacea* preferentially over *Marisa* and had difficulties extracting *Marisa* from its shell. They also failed to extract some large specimens of *P. chemnitzi*. Failures with both species were apparently related to problems in removing opercula. These observations indicate that *R. sociabilis* can no longer be considered a strict specialist on *Pomacea*. *Received 21 August 1979, resubmitted 8 April 1982, accepted 15 October 1982.*

MOLLUSKS are a major dietary component for a surprisingly diverse assemblage of birds, including various ducks, shorebirds, rails, storks, and raptors (Snyder 1967). Of particular interest, because of its endangered status in the United States, is the Snail, or Everglade, Kite (*Rostrhamus sociabilis*), a species renowned for its dependence on fresh-water snails of the genus *Pomacea*. Snyder and Snyder (1969) discussed some of the peculiar anatomical and behavioral specializations of the Snail Kite that enable it to feed on *Pomacea paludosa* in Florida. Here, we present information on interactions of the species with snails of northern Colombia, as observed 28 April to 5 May 1978, the start of the rainy season.

Our study area was a backwater of the Río Magdalena next to the Barranquilla airport. Two large snails of the family Pilidae were found in abundance here, *Pomacea chemnitzi* and *Marisa cornuarietis*. *Pomacea chemnitzi*, with its shallow spire, closely resembles *P. paludosa* in shape, but, at least in this locality, it commonly reaches a size considerably larger than typical individuals of the Florida species. *Marisa cornuarietis* is coiled in a plane and looks like a giant ramshorn snail, but, like *Pomacea*, it possesses a hard operculum with which it can close off the entrance of the shell.

RESULTS

Snail Kites characteristically bring their prey to conspicuous feeding perches for extraction procedures, and the shells accumulating underneath give a record of the foods eaten. We soon learned, however, that some shell piles in the study area yielded biased representations of kite diet because of differential losses of shells after deposition. Shell piles under perches standing in water retained their *Marisa* shells well but lost most of their *Pomacea* shells, apparently because the former are heavily calcified and tend to sink, while the latter readily float and can drift away on water currents. Thus, for example, we found only 28 *Pomacea* shells among 699 *Marisa* shells at one perch that obviously had been inundated recently.

In contrast, we found a preponderance of *Pomacea* over *Marisa* in shell piles above the water line. The overall *Pomacea* to *Marisa* ratio at four such perches was 3.0, and it varied from 1.8 to 7.2 among the perches (Table 1). The four perches were located within 100 m of each other in an area of mixed brushy swamp and flooded pasture immediately adjacent to an active kite nesting colony. Using the perches were a minimum of three brown-plumaged kites (females and/or young males).

Under all four of the above perches we were surprised to find evidence that the kites were failing to extract some *Pomacea* and *Marisa*, as we found whole uneaten individuals of both species, some still alive and others in various stages of decay. In addition, an inspection of the shells revealed that many of the snails were

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Table 1. Shells found under active perches of Snail Kites in Colombia.[a]

	Perch number				Total shells
	1	2	3	4	
Pomacea chemnitzi					
Empty shells	35	35	28	28	126
Shells with viscera	5	15	2	5	27
Whole snails	6	1	6	1	14
Total shells	46	51	36	34	167
Marisa cornuarietis					
Empty shells	5	1	0	5	11
Shells with viscera	7	7	1	8	23
Whole snails	5	6	4	6	21
Total shells	17	14	5	19	55
Pomacea/Marisa ratios	2.7	3.6	7.2	1.8	

[a] All shell piles above the water line.

only partially eaten (Table 1). The failure rates for the two snail species were highly significantly different ($\chi^2 = 25.47$, df = 1, $P < 0.001$). Of 167 *Pomacea* shells only 14 (8%) still contained whole, uneaten snails, compared to 21 of 55 *Marisa* shells (38%).

In the cases of uneaten *P. chemnitzi,* failure appeared to be related to snail size (Fig. 1A), as uneaten snails (averaging 57.2 mm in greatest length) were significantly different in length from eaten snails (averaging 52.8 mm), as shown by a Mann-Whitney *U*-test ($t_s = 3.182$, $P < 0.005$). Opercula of the uneaten specimens were scratched with the usual bill marks one finds on kite-extracted *Pomacea*. Apparently, the kites had tried to extract the uneaten *Pomacea* but had failed to grasp the opercula or had been unable to pull the opercula free from the snails. In watching several unsuccessful attempts, we saw no signs that the birds might have been deliberately rejecting individual snails that were noxious to them. The kites simply worked away at these snails with their bills in the usual fashion, appeared to lose interest after a few minutes, and eventually allowed the snails to fall from the perches.

The failure of the kites to extract all *P. chemnitzi* bears further comment. With *P. paludosa* in Florida we have never, in many hundreds of direct observations, seen an adult kite fail, and only very rarely have we found evidence of less than complete extractions of softparts. For example, of 529 *P. paludosa* shells collected from beneath a perch being used exclusively by adult and subadult kites on Lake Okeechobee in February 1979, only four still contained small fragments of snail viscera. On the other hand, recently fledged Florida Snail Kites do fail occasionally in extractions of *P. paludosa*. For example, on 21 May 1979 we collected shells from a screen installed below a perch being used almost exclusively by banded kites less than 2 months beyond fledging age. Of the 114 shells collected, 9 (7.9%) contained whole, unextracted snails. The uneaten snails did not differ significantly in size from eaten snails ($t_s = 1.524$, $0.10 < P < 0.20$; Mann-Whitney *U*-test), and, in the cases in which we directly observed young kites dropping whole snails at perches, the cause was quite clearly nothing more than clumsiness. The birds had obvious difficulties holding the snails properly in their feet and sometimes lost control of the shells in attempting to position them.

Whether the failures of Colombian Snail Kites in extraction of *P. chemnitzi* might similarly be related to the age of the kites is conjectural. The kites we observed at the perches were all brown-plumaged and none appeared to be mated—characteristics consistent with youth. All were fully independent, however, and none was clumsy in its snail-extraction efforts. These factors, together with the size-dependence of their failures with *P. chemnitzi,* suggest that their difficulties may have resulted from more than just inexperience. In any event, we believe it would be unwise to assume that the few birds we observed were representative of the kite population as a whole.

Failures with *M. cornuarietis,* like failures

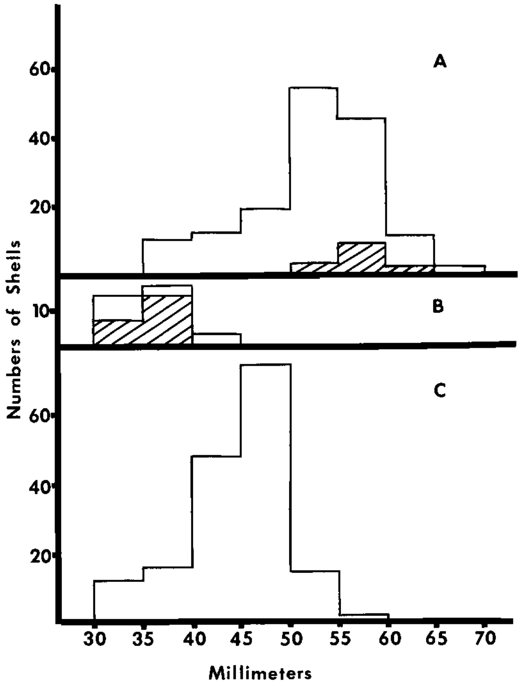

Fig. 1. Size distributions of *Pomacea chemnitzi* and *Marisa cornuarietis* shells found under active perches of Snail Kites: A, greatest length of eaten (clear) and uneaten (shaded) *Pomacea chemnitzi*; B, greatest diameter of eaten (clear) and uneaten (shaded) *Marisa cornuarietis*; C, greatest diameter of all *Pomacea chemnitzi*.

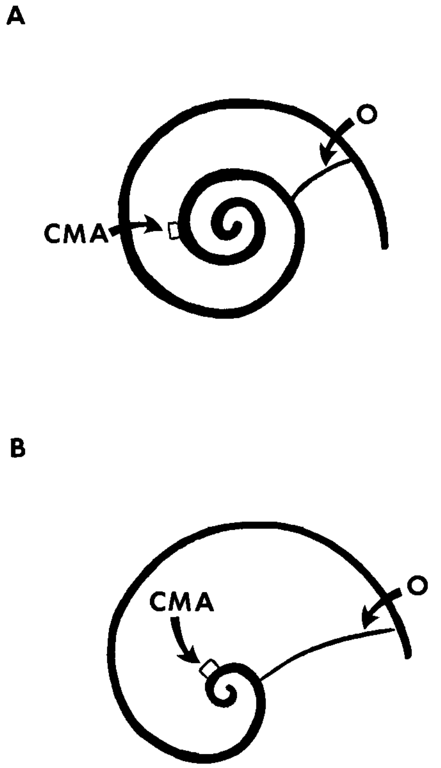

Fig. 2. Diagrammatic representation of position of columellar muscle attachment (CMA) and operculum (O) of: A, *Marisa cornuarietis*; B, *Pomacea chemnitzi*.

with *P. chemnitzi*, appeared to be caused by an inability of the kites to remove opercula, as the opercula of whole, uneaten snails under perches showed clear scratch marks. The high frequency of failure may have been due to this snail's ability to pull far back into its shell: in *Pomacea* the operculum usually forms a tight fit just inside the aperture; in *Marisa* the operculum can be withdrawn for a considerable distance inside where it is difficult to grasp. Failure with *Marisa* was not a function of snail size, as unextracted snails did not differ significantly in maximum diameter from extracted snails ($t_s = 0.468$, $P > 0.5$; Mann-Whitney *U*-test).

Even when kites were able to remove the opercula of *Marisa*, they commonly failed to get more than the foot of the snail out of the shell, probably because the columellar muscle attachment of this snail is about as far inside the entrance as the long hooked bill of the birds can reach (Fig. 2A). This muscle attachment, which must be severed to allow a complete extraction of the softparts, lies much closer to the entrance in *Pomacea* (Fig. 2B). The great majority of *P. chemnitzi* from which kites were able to remove opercula were fully extracted (126 of 153 cases). By comparison, only 11 of 34 *Marisa* from which the opercula had been removed were fully extracted, a highly significantly difference ($\chi^2 = 33.0$, df = 1, $P < 0.001$). Generally, the softparts of *Marisa* snails were broken near the columellar muscle attachment, and all of the viscera remained in the shells. Breakage probably resulted from the kites' pulling on the softparts from the shell entrance after failing to sever the columellar muscle.

Direct observations of the snail-extraction behavior of the minimum of three kites using the active perches listed in Table 1 confirmed a higher success rate with *Pomacea* than with *Marisa*, although the success rates were not significantly different ($\chi^2 = 1.13$, df = 1, $0.25 < P < 0.50$) for the two snails, probably due to small sample size. Of six cases of the kites attempting to extract *Marisa*, only two were successful to the point of the birds' getting some meat out of the shell. With *Pomacea* the success rate was eight of 11 attempts.

Not only were the kites failing more frequently with *Marisa* than with *Pomacea*, they were also receiving much less reward from this snail when successful. The wet weight of a *Marisa*'s softparts generally does not exceed 2 g, whereas a typical *P. chemnitzi* yields 15–20 g of meat. When the total and partial failure rates in extractions from Table 1 are included in calculations, the yield in soft tissues from an average *P. chemnitzi* runs about 15 times as great as from an average *M. cornuarietis*.

From the above comparison one might expect to find the kites selectively foraging for *Pomacea* in preference to *Marisa*. That this might be true was apparent from an inspection of foraging areas near the active feeding perches. In walking several transects through the marsh we were able to tally between 10 and 20 times as many adult *Marisa* as *Pomacea* near the water surface (where they would be vulnerable to the kites). Yet, we found a *Marisa* to *Pomacea* ratio of about 1:3 at the four feeding perches and directly observed a 6:11 *Marisa* : *Pomacea* capture ratio near the perches.

One may question why the kites were taking *Marisa* at all in view of its much inferior reward potential. Possibly, the captures of *Marisa* represented nothing more than mistakes in discrimination between the two snails. From the 3–6-m heights at which the kites generally forage, distinguishing between *Pomacea* and *Marisa* may present problems, especially when shells are covered with algae. Once a kite has gone to the trouble of capturing the "wrong species," the reward, though relatively low, may still be high enough to justify an extraction attempt rather than a rejection and a continued search for *Pomacea*. Also, assuming the observed 10–20-fold superiority in abundance of *Marisa* over *Pomacea* might apply inversely to the time and energy investment needed to locate the two snails, the net reward superiority of a typical *Pomacea* over a typical *Marisa* may be far less than that calculated above for snails already captured. Unfortunately, we did not record information on the average time it takes to capture the two snail species, so we could not evaluate this question in any direct fashion.

The size distributions of captured *Pomacea* and *Marisa* snails in Fig. 1A and B are presented in terms of maximum linear dimensions: total length from top of spire to base of aperture for *Pomacea* and greatest diameter for *Marisa*. In these terms the sizes of some *Marisa* shells fall below the sizes of all *Pomacea*. At first sight it might seem puzzling that the kites captured the smallest *Marisa*, because they were apparently rejecting *Pomacea* of similar linear extent (but much greater mass). Under field conditions, however, the maximum linear dimensions of a *Pomacea* will often be hidden from the view of a kite flying overhead, because snails near the water surface are not always oriented the same way with respect to gravity. In fact, a *Pomacea* viewed by looking down on its spire looks very much like a *Marisa*, and in this orientation its greatest visible linear dimension is a maximum diameter, not a total length. If instead of plotting *Pomacea* according to total length, we plot these snails according to greatest diameter (Fig. 1C), we find that the *Pomacea* curve now overlaps the *Marisa* curve completely. Thus, the potential ease of discrimination between the smallest *Pomacea* captured and the smallest *Marisa* captured disappears.

DISCUSSION

The extractions of *P. chemnitzi* by Snail Kites followed the pattern described by Snyder and Snyder (1969) and supported by Voous and Van Dijk (1973). They bore no resemblance to the extraction procedures described by Lang (1924) and Murphy (1955). We have now observed kites eating three different species of *Pomacea* (including *P. dolioides*, on which Lang's description was based), and all have been handled in the same way: removal of the operculum with the bill, cutting of the columellar muscle attachment with strokes of the upper bill, and pulling of the freed softparts out of the shell with the bill. Unlike Lang and Murphy, we have not seen kites waiting for voluntary extension of snails from their shells, we have no evidence that they ever ingest opercula in the wild, and we have seen nothing to suggest that they pierce the snails in a "nerve plexus," causing the snails to release their holds on their shells. We believe that the Lang-Murphy description, while colorful, is incorrect. Unfortunately, this description has become entrenched in the popular literature on kites and may never be evicted, as there are now so many references reiterating it.

On several occasions we observed Snail Kites discarding the yolk glands of female *P. chemnitzi,* and we found discarded yolk glands of this species under kite feeding perches. Very likely the yolk and eggs of this snail are highly distasteful, as are the yolk and eggs of *P. dolioides* and *P. paludosa,* which are also commonly rejected by the kites and other predators (see Snyder and Snyder 1969, 1971). Like the orange eggs of *P. dolioides* and the pinkish-white eggs of *P. paludosa,* the yellowish-white eggs of *P. chemnitzi* are conspicuous and presumably aposematic. All three species lay their eggs out of the water on emergent vegetation.

Marisa cornuarietis, in contrast, has aquatic eggs, which are not highly conspicuous. We did not note discarded *Marisa* yolk glands under kite perches and have no direct evidence that the yolk and eggs of this species might be distasteful.

Although with most fresh-water snails there is little evidence that opercula might serve as an effective adaptation to thwart predators (see Snyder 1967), the opercula of both *M. cornuarietis* and *P. chemnitzi* appear to have value in reducing kite predation in Colombia. Some kite perches are over water, and snails that are not successfully extracted by kites get a second chance at life if they fall back into the water on being discarded. To our knowledge, the only predators of fresh-water molluscs known to be regularly deterred by snail opercula are sciomyzid fly larvae (see Berg 1961).

Although Snail Kites have been seen taking nonsnail prey under conditions of extreme food shortage (Sykes and Kale 1974), the observations reported in this paper are the first of the species feeding on a genus of snail other than *Pomacea.* It is uncertain, however, whether or not kites are successful enough with *Marisa* to be able to exist on it alone in areas where *Pomacea* does not occur. *Marisa* was introduced into southern Florida over 20 yr ago (see Edmondson 1959) and has fairly recently spread out into regions where Snail Kites occur. It is not yet abundant there, but is widespread—we have seen shells along the Tamiami Trail and as far north as Everglades Holiday Park near Alligator Alley. To date we have not found any of its shells at kite feeding perches. As studies of *M. cornuarietis* have shown the species to have complex competitive and predatory relationships with other snail species (see Demian and Lutfy 1965, Ruiz-Tibén et al. 1969), the establishment of *Marisa* may prove to be a mixed blessing for the Snail Kites of Florida.

ACKNOWLEDGMENTS

Our studies in Colombia were made possible by support from the U.S. Fish and Wildlife Service and the Dade County, Florida Aviation Department. The primary purpose of the trip was a study of the impact of the Barranquilla airport on the nearby Snail Kite populations. We thank Bonnie Ann Frank, David Dahmen, Edgar de Castro, and German Solano for assistance rendered in field studies in Colombia and Steven Beissinger and Gary Falxa for assistance in kite studies in Florida. Alan Solem of the Chicago Field Museum identified the *Pomacea* snails.

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BEHAVIOR, MORPHOLOGY, AND SYSTEMATICS OF *SIRYSTES SIBILATOR* (TYRANNIDAE)

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Abstract.—Field and laboratory studies support recent hypotheses that *Sirystes sibilator* is closely allied with the myiarchine flycatchers rather than with *Tyrannus* or with the cotingids. The first confirmed nest of this tyrant (located in a natural tree cavity), its foraging behavior, and the derived character states of the nasal septum and of the syrinx argue convincingly for its placement in an assemblage with *Myiarchus, Rhytipterna,* and *Casiornis.* Data, still lacking, on the color of the eggs and nature of the nest lining are needed for *Sirystes* (and for *Rhytipterna* and *Casiornis*) before consideration can be given to the generic relationships within the myiarchine flycatchers. *Received 1 February 1982, accepted 16 July 1982.*

The systematic position of the Sirystes (*Sirystes sibilator*), traditionally placed in its own monotypic genus, has been enigmatic for decades. Though included in the family Cotingidae by Ridgway (1907), largely on the basis of the scutellation of the tarsal envelope, *Sirystes* has been considered a tyrant flycatcher by Hellmayr (1927) and subsequent authors. Hellmayr allied it with the *Tyrannus* group, but Traylor (1977), influenced by Warter's (1965) study of the tyrannoid skull, placed it in the *Myiarchus* group. On the basis of syringeal characters, Ames (1971) was unable to place it with conviction in any of his "structural groups" of tyrannids.

This paper was prompted by Fitzpatrick's discovery of the first confirmed nest of *Sirystes*, to which description he has added behavioral observations made in recent years. Lanyon has contributed an analysis of cranial and syringeal morphology, part of a more general study of the putative relatives of *Myiarchus.*

Behavior

Sirystes is a regular but uncommon inhabitant at the Cocha Cashu Biological Station, located in the Manu National Park, dept. Madre de Dios, Peru (11°55'S, 71°18'W, elev. 380 m). It forages almost exclusively in the high canopy of the alluvial plain forest bordering the meandering Manu River (Terborgh et al. in press). Mean foraging heights for 21 independent sightings in 1976 and 1977 was 38 ± 8.5 m in a forest whose average canopy treetop is between 40 and 45 m (unpubl. data). *Sirystes* here appears to prefer primary, dry-ground forest to other, more inundated forest types, and it shows an unusual propensity for foraging in tall, emergent trees adjacent to treefalls.

Sirystes forages in a fashion virtually identical to the unusual style of *Myiarchus,* especially in its frequent use of outward and downward hovergleaning (Fitzpatrick 1980, unpubl. notes). Moreover, while searching the surrounding vegetation, *Sirystes* uses the peculiar posture typically associated only with the genus *Myiarchus.* The head is held out horizontally, stretched away from the body in more exaggerated fashion than in other flycatchers. Perhaps for this reason, the throat and crown feathers are often erected, giving the bird a large headed, "throaty" silhouette. Again in conjunction with these habits, both *Sirystes* and *Myiarchus* peer about and slowly bob the head in more deliberate fashion than any other flycatcher (except in the unrelated genus *Mionectes*). Members of the genus *Myiarchus* are among the few tyrannids that habitually "pop" the bill loudly while being held in the hand after removal from a mist-net. Although the significance of this behavior is obscure at best, it may be worthy of note that a *Sirystes* removed from a mist-net (also at Cocha Cashu) repeatedly popped its bill while being banded and photographed.

The typical daytime vocalization given during active foraging is a clear, ringing "wher-péw." During more intense calling, intrapair displaying, and dawn-singing, this frequently is lengthened into "wher-pe-pep-pep-pew-pew

Fig. 1. View from ground of *Sirystes sibilator* nest site (white arrow near center) in emergent *Calicophyllum* tree, well above nearby forest canopy (dark vegetation to lower right and upper left). Note unusually open surroundings at nest height amidst several old treefall openings.

. . . pew." On the morning of 2 October 1981, incessant repetitions of this latter song, in an area known even in previous years to be frequented by a pair of *Sirystes,* attracted JWF's attention to two birds high in a 45-m *Calicophyllum spruceanum* tree (Rubiaceae) adjacent to a slightly overgrown treefall clearing (Fig. 1). Both birds were bobbing and flitting excitedly from perch to perch with their slightly elongated crown feathers raised into vague "crests." One bird was carrying in its bill a large wad of dark material, apparently insects. Several minutes later, the bird carrying prey disappeared into a hole along a major limb high in the tree. It remained out of sight about 1 min, then flew back out, sat briefly a few meters above the hole, then flew off to forage elsewhere. From 0755 to 0941 a total of 12 such nest visits occurred, the intervals between visits averaging 8.6 min (shortest interval 1 min, longest 16 min). Both birds visited the nest with food, frequently calling loudly together in the nest tree. They appeared to be foraging up to 200 m from the nest tree, although they almost invariably continued to sally after prey items high in the nest tree itself, even while carrying large boluses of food. Twice, the birds returned simultaneously to the nest tree; one waited perched on twigs outside the hole, while the other entered and exited. Nest visits varied from just a few seconds up to about 1 min. One fecal sac removal was observed.

The nest site was determined through telephoto lenses to be about 32 m above the ground. In comparison with the birds' body sizes the hole appeared to be at least 15 cm wide, perhaps larger. It was at the base of a nearly perpendicular "elbow" in the tree limb, with the hole running roughly horizontally into the main branch. An old break had rotted out to create the cavity, and it left a 6- to 8-cm long lip rimming the lower edge of the hole. The depth of the hole, penetrating horizontally into the limb, could not be determined, nor could any features of nest construction or contents be seen. *Calicophyllum* trees are known locally as "Palo Calato" ("naked pole") because of their extraordinarily smooth, seemingly barkless appearance (Fig. 1). This makes the trunk and limbs extremely slippery and difficult to climb, presumably for predators as well as for humans.

Judging from the frequency of nest visits and the large size of the food boluses brought in on 2 October, the nest must have contained well-developed nestlings. Fitzpatrick left the study site the following day, but N. Pierpont reported nest visits by both birds on 3, 4, and 5 October. Thereafter, no further activity was observed at the nest. Early on 6 October, at least two *Sirystes* were heard actively calling about 100 m from the nest. They did not come near the nest tree during a 20-min observation period there (1450–1510) nor on two subsequent days. Assuming the nestlings fledged successfully, they apparently did so on 5 or 6 October.

The only previous, published information on the nesting habits of *Sirystes* is Wetmore's (1972: 436) reference to birds in Panama "occasionally examining cavities in tree trunks."

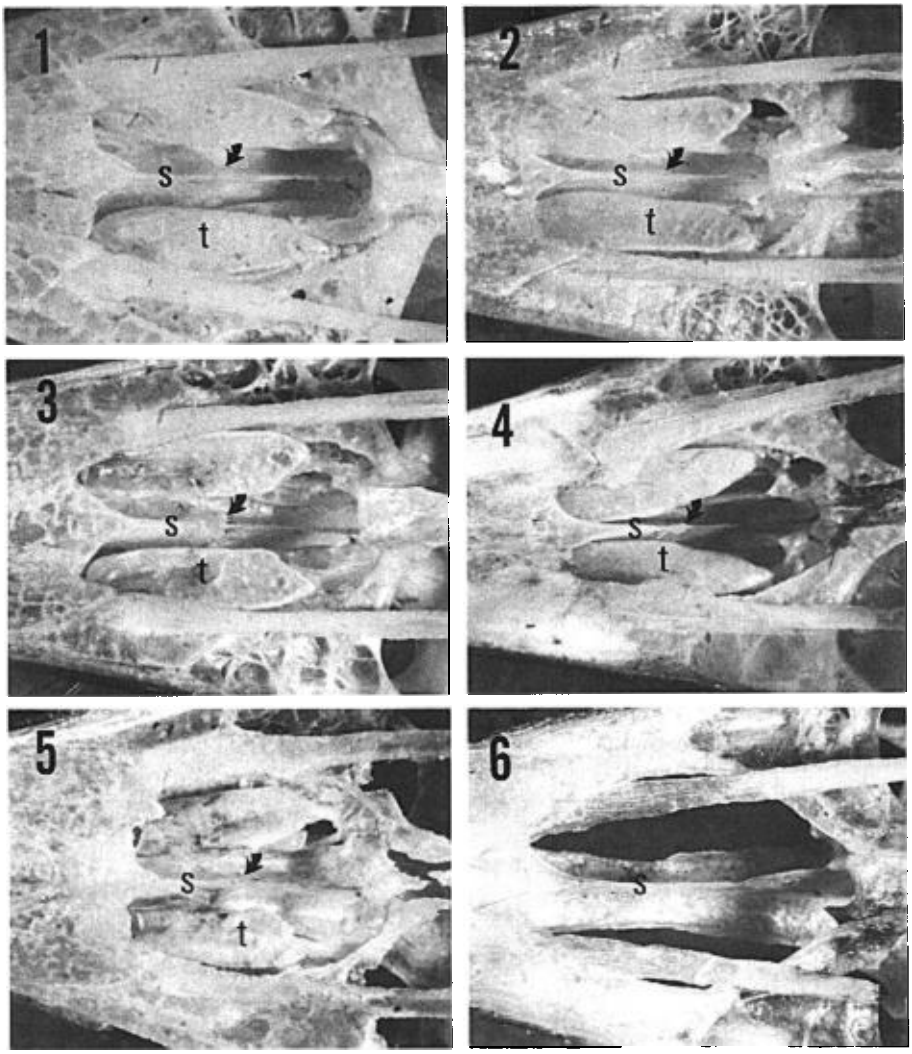

Fig. 2. Photographs, taken through a dissecting microscope, of the ventral aspect of the nasal region of the skulls of some tyrannine flycatchers (anterior end of the skull to the left): 1. *Sirystes sibilator* (USNM 347723); 2. *Myiarchus tuberculifer* (AMNH 7175); 3. *M. cephalotes* (AMNH 9248); 4. *Rhytipterna immunda* (AMNH 11617); 5. *Deltarhynchus flammulatus* (AMNH 11391); 6. *Attila cinnamomeus* (AMNH 11615). Arrows indicate the internal supporting rod present in all skulls except that of *Attila*; the knife-like ventral edge of the ossified nasal septum, s, lacks a trabecular plate; ossification of the nasal capsule includes the alinasal turbinals, t, in all skulls except that of *Attila*. All specimens magnified 16×.

MORPHOLOGY

Sirystes differs from most *Myiarchus* in possessing a complete suture along the outer edge of the tarsus as well as the usual full inner suture (i.e. tarsus holaspidean, not exaspidean). This arrangement of the tarsal envelope was the principal basis for Ridgway's (1907) placement of *Sirystes* in the Cotingidae, but Ridgway admitted that "the bill [of *Sirystes*] is typically tyrannine, resembling closely that of *Tyrannus* and the stouter billed *Myiarchi*." The striking black-and-white plumage pattern of *Sirystes*, with diffuse olive dorsal streaks, also differs from the familiar and remarkably uniform plumage pattern of most *Myiarchus.* The rectrices and wing coverts of the juvenal plumage of *Sirystes* are fringed with Antique Brown (Smithe 1975), though this color is lacking in the adult plumage. This is a pattern characteristic of all species of *Myiarchus,* including those species in which Antique Brown is lacking in the adults.

Recent anatomical studies involving the skull (Warter 1965) and the syrinx (Ames 1971) have indicated the effectiveness of these structures in determining relationships within the suboscines. Two complexes in particular have already proven useful in diagnosing *Myiarchus* flycatchers and their relatives: (1) the nasal septum, and specifically the degree to which there is ossification and buttressing with internal supporting structures, and (2) the number, shape, and position of the internal cartilages of the syrinx (Lanyon 1982).

The nasal capsule of *Sirystes* (Fig. 2, number 1) is typically tyrannine (as defined by Traylor 1977), in that the nasal septum is well-developed (ossified) but lacks a trabecular plate along the ventral edge. The nasal septum is buttressed by a well-developed internal supporting rod, identified with an arrow in Fig. 2. This derived state of the nasal septum, found in *Sirystes,* is shared with *Myiarchus* (20 of the 22 species; two still unavailable), *Rhytipterna* (all three species), *Casiornis* (both species), and *Deltarhynchus* and is not found in any of the remaining genera placed in the Tyranninae by Traylor (Lanyon 1982, unpubl. notes). Note the lack of an internal supporting rod in the nasal septum of *Attila* (Fig. 2, number 6).

Sirystes shares a suite of syringeal characters with *Myiarchus* (15 species examined thus far), *Rhytipterna* (all three species), and *Casiornis* (both species examined) that sets these genera apart from all other tyrannids (Lanyon 1982, unpubl. notes). In these four genera there are two pairs of cartilages that lie within the internal tympaniform membranes: (1) a large, dorsal pair, which are J- or L-shaped and are connected anteriorly to the ventral segment of the tracheo-bronchial junction (with no connection to the dorsal ends of the A-2 semirings), and (2) a much smaller, ventral pair, of variable shape and located within the membranous connections that extend between the posterior ends of the large cartilages and the ventral ends of the B-2 bronchial semirings. In Fig. 3 we compare the number, shape, and location of these internal cartilages as seen in *Sirystes,* in three other myiarchine flycatchers (*Myiarchus ferox, M. oberi,* and *Rhytipterna holerythra*), and in two other tyrannines (*Deltarhynchus flammulatus* and *Attila cinnamomeus*).

The large cartilages are J-shaped in *Sirystes* and the other myiarchine flycatchers, and their anterior ends are connected to the ventral segment of the tracheo-bronchial junction, at some distance from the dorsal ends of the A-2 semirings. The large cartilages do not have this characteristic shape in *Deltarhynchus* and *Attila,* where they can be seen to connect to the dorsal segment of the tracheo-bronchial junction and the dorsal ends of the A-2 semirings. The smaller, ventral pair of cartilages is lacking in the syrinx of *Deltarhynchus.*

The method of dissection and terminology follow Ames (1971).

Discussion

The behavioral features described above, even down to the quality of the song, once confused no less capable a field ornithologist than the late Paul Schwartz with regard to birds that he had recorded but not collected along the Rio Masparro, Barinas, Venezuela. The recordings had been deposited with the Library of Natural Sounds at Cornell University's Laboratory of Ornithology and filed as "*Myiarchus ferox,*" but Lanyon wrote Schwartz that they could not have been made from any species presently regarded as *Myiarchus.* Six months later Schwartz replied: "The birds from the Rio Masparro I've now definitely identified as *Sirystes sibilator.* I feel embarrassed, but not terribly so. If you already know the bird or if you some day experience it I'm sure you'll know what I mean. In size, shape, attitudes and actions this bird is extremely *Myiarchus*-like rather than like the group with which it is presumed to be related [the *Tyrannus* group] . . . . I recently encountered the bird again down near Burgua, alerted by the voice. Here again I was convinced they were *Myiarchus* for the same reasons, until with playback I finally got them to where the sun was at my back and they were against a foliage background. . . . I collected one just as a clincher." Schwartz's field experience, though anecdotal and unconvincing by itself, was of sufficient importance to alert both of us to the need for further information about this species.

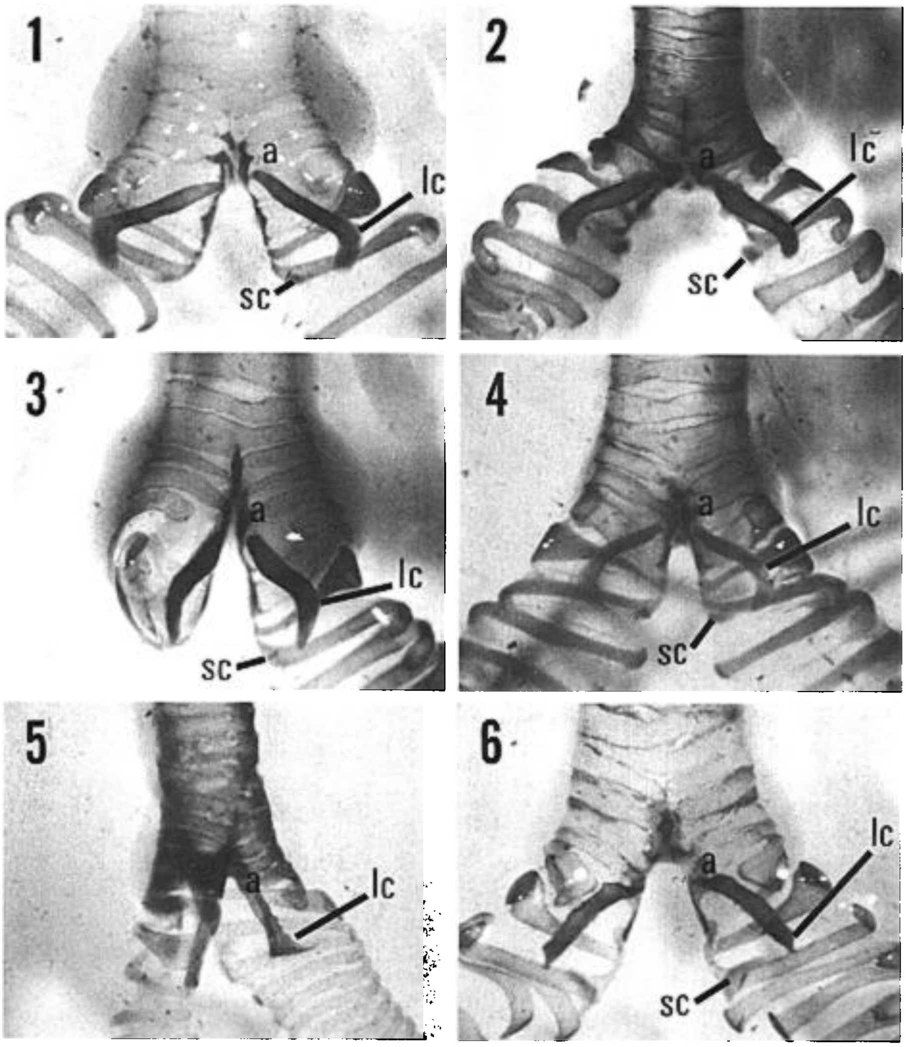

Fig. 3. Photographs, taken through a dissecting microscope, of the dorsal aspect of the syringes of some tyrannine flycatchers: 1. *Sirystes sibilator* (YPM 2791); 2. *Myiarchus ferox* (AMNH 8112); 3. *M. oberi* (AMNH 6677); 4. *Rhytipterna holerythra* (AMNH 8260); 5. *Deltarhynchus flammulatus* (AMNH 8128); 6. *Attila cinnamomeus* (AMNH 8126). Large cartilages, lc; small cartilages, sc; dorsal end of A-2 semirings, a. All specimens magnified 19×.

Cavity-nesting is a rare and almost certainly derived condition in the Tyrannidae, being most prevalent in the genus *Myiarchus* and its close relatives (Lanyon 1978, 1982). *Casiornis* has been reported to be a cavity nester, but the eggs and nest lining have not been described (*fide* Helmut Sick pers. comm.). The nesting habits of the three species of *Rhytipterna* are still unknown, but, on the basis of derived morphological and behavioral characters shared with *Myiarchus*, one would hypothesize that they too are cavity-nesters and have eggs like those of *Myiarchus*. That *Sirystes* is now known to be a cavity-nester lends support to the hypothesis (Traylor 1977, Lanyon 1982) that *Sirystes* is a close relative of *Myiarchus*.

The nest lining of *Myiarchus* is unique among the 12 genera of tyrants in which nesting in tree cavities has been reported, bearing in mind that we still lack complete data for

Rhytipterna, Casiornis, and *Sirystes.* Invariably, the lining consists of quantities of fur and feathers, in addition to vegetable fibers, and frequently there are fragments of shed reptilian skin or plastic and paper substitutes (Lanyon 1978, unpubl. notes). These unique contents of the nest lining form an important part of the generic diagnosis of *Myiarchus,* for they help to embrace three of the more "aberrant" species formerly placed in monotypic genera: *semirufus, validus,* and *magnirostris.* Because no details could be obtained regarding the nest lining or the color pattern of the eggs in the single nest record reported here, the generic relationship of *Sirystes* and *Myiarchus* remains uncertain. Indeed, on its own, the cavity-nesting behavior of *Sirystes* could be a simple case of convergence, as it most certainly is in the case of *Colonia* (subfamily Fluvicolinae).

The scutellation of the tarsal envelope, once given considerable weight in the classification of the suboscines, has been shown to be more variable within genera and families than even Ridgway (1907: 328–329, 336) would admit, and several workers have cautioned against placing undue reliance on this character (Lanyon 1967, Ames et al. 1968, Snow 1973, Zimmer unpubl. notes). We are reminded that *Myiarchus validus* was at one time placed in a monotypic genus and transferred to the Cotingidae because the tarsal envelope was nonexaspidean (Ridgway 1906). Indeed, the suggestion by Warter (1965) and Ames (1971) that *Rhytipterna, Casiornis,* and *Attila* be transferred from the Cotingidae to the Tyrannidae has been followed for Peters' Check-list (Snow 1973, Traylor 1977), even though the tarsal scutellation of these genera is nonexaspidean.

Virtually every feature of the plumage color and pattern of *Sirystes* can be found within the genus *Myiarchus*: the dark cap and contrasting pale back characterizes the Andean populations of *tuberculifer,* the pale-tipped rectrices are found in *apicalis,* and the gray and white underparts distinguish *sagrae* and *antillarum.* Even the white rump patch and extensive white in the wings, so conspicuous in northern *Sirystes,* virtually disappear in the southernmost populations of the species. With full cognizance of the range of variation within the 22 species of *Myiarchus,* it becomes difficult to argue against merger of *Sirystes* and *Myiarchus* on the basis of plumage color and pattern.

Ames (1971) concluded that "the syrinx of *Sirystes* is typically tyrannid in cartilages and musculature with little similarity to the simple syringes of the Cotingidae," but questioned Hellmayr's (1927) placement of the species with the *Tyrannus* group, because it lacks almost all of the syringeal features of that assemblage. Lanyon agrees with Ames on both of these points but has difficulty reconciling Ames' failure to recognize the syrinx of *Sirystes* as typically myiarchine. The single specimen initially available to Lanyon agrees in all respects with the syringes of *Myiarchus, Rhytipterna,* and *Casiornis*; it could not with certainty be separated from a series of syringes taken from those three genera. Ames did not stain his specimens for bone and cartilage and consequently may have overlooked some of the critical myiarchine characters. He kindly loaned his two specimens of *Sirystes* to Lanyon and gave permission for them to be stained with alcian blue and alizarin red (after Dingerkus and Uhler 1977). These two specimens were found to share the same derived complex of syringeal characters that distinguishes the myiarchine assemblage from all other tyrannids.

Although we believe the affinities of *Sirystes* with the myiarchine group of tyrannines to be unequivocal now, we recommend caution in any revisionary consideration of the generic relationships among *Sirystes, Myiarchus, Rhytipterna,* and *Casiornis.* Descriptions of the color and markings of the eggs and of the nature of the nest lining, still lacking for all but *Myiarchus,* are needed before we can adequately address the problem of generic limits and devise a meaningful phylogeny for this group.

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THE FUNCTION OF SINGING IN FEMALE BLACK-HEADED GROSBEAKS (*PHEUCTICUS MELANOCEPHALUS*): FAMILY-GROUP MAINTENANCE

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Abstract.—The responses of young Black-headed Grosbeaks (*Pheucticus melanocephalus*) to playback of the songs of parents and strangers were examined. I found that young grosbeaks moved about more, called more, and were more often oriented toward speakers in response to parental song (both male and female) than in response to the songs of strangers. I suggest that such a response is part of a system used by Black-headed Grosbeaks to maintain family groups after the young fledge. In this system, an adult with food, but unaware of the location of its young, sings to elicit begging from its young. The parent bird is then able to locate and feed its young. *Received 31 August 1981, accepted 26 May 1982.*

Among passerines, song is typically the function of the male. There is also much evidence, however, of regular, occasional, and artificially induced song by females. It has long been recognized, for instance, that females of many species can be induced to sing by injection of testosterone (Baldwin et al. 1940, Kern and King 1972). There are also many reports of species in which the female sings only in exceptional cases, e.g. the Western Meadowlark (*Sturnella neglecta*; Lanyon 1957), Indigo Bunting (*Passerina cyanea*; Nolan 1958), Song Sparrow (*Melospiza melodia*; Van Tyne and Berger 1976), Eastern Phoebe (*Sayornis phoebe*; Smith 1969), Eastern Bluebird (*Sialia sialis*; Morton et al. 1978), and White-crowned Sparrow (*Zonotrichia leucophrys*; Kern and King 1972). In other species, singing appears to be a regular feature of female behavior, i.e. many species have been reported in which females commonly sing in a variety of situations (Table 1).

Despite these many observations, the significance of singing in females remains obscure. Possible functions, however, have been postulated. Armstrong (1963) suggested that antiphonal singing is a "means whereby contact, *rapport*, and the social bond are maintained." Duetting is believed to be important in the synchronization of breeding behavior and in the reinforcement of the pair bond (e.g. Thorpe and North 1965, Thorpe 1966, Hooker and Hooker 1969, Bertram 1970, Payne 1971). Concerning instances of female singing other than antiphonal singing or duetting, Kern and King (1972) have suggested a number of functions, including stimulating the breeding activities of the male. Nottebohm (1975) suggested that singing by females may influence a bird's socialization and choice of partner and, in some cases, aid in territorial defense.

Among the species of birds in which singing by females has been reported is the Black-headed Grosbeak (*Pheucticus melanocephalus*; see Fig. 1). Weston (1947), in a general study of the breeding behavior of the grosbeak, reported that females sang "while incubating or brooding, usually as the male comes to take his place on the eggs or young. Several times during nest-building, the female uttered songs in the vicinity of the nest and always in the presence of the male. The female will also occasionally sing while foraging in the peripheral foliage of trees, but only when the male is close by." Armstrong (1963) stated that singing by females tends to be characteristic of cardueline finches. Van Tyne and Berger (1976: 249), in a general discussion of female song, suggested that the songs of the female Black-headed Grosbeak are nearly as elaborate as those of the male.

Despite these observations, the function of female song in the Black-headed Grosbeak, as in other species, is unclear. The present study is an attempt to ascertain the function(s) of this song. The initial year of this 2-yr study was devoted to extensive field observation and re-

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TABLE 1. Reports of singing in females among various avian species.

	Situations in which female sings[a]					Suggested function(s)[a]				
Species	NB	NR	I	B	FY	TD	PB-M	C	F-GM	Source
Greenshank *Tringa nebularia*					X					Simms 1958
European Nightjar *Caprimulgus europaeus*		X								Selous 1905
Gray-capped Flycatcher *Myiozetetes granadensis*			X		X					Skutch 1953
Loggerhead Shrike *Lanius ludovicianus*						X				Armstrong 1963
European Dipper *Cinclus cinclus*							X	X		Van Tyne and Berger 1976
American Dipper *Cinclus mexicanus*			X			X				Bakus 1959a, b
House Wren *Troglodytes aedon*			X		X				X	Armstrong 1955
Wrentit *Chamaea fasciata*						X				Armstrong 1963
Blue Wren *Malurus cyaneus*								X		Robinson 1949
Paradise Flycatcher *Terpsiphone viridis*			X							Moreau 1949
Elepaio *Chasiempis sandwichensis*	X		X	X				X		Conant 1977
Willie Wagtail *Rhipidura leucophrys*						X				Robinson 1949
White-crowned Sparrow *Zonotrichia leucophrys*							X	X		Blanchard 1941, Kern and King 1972
Grasshopper Sparrow *Ammodramus savannarum*		X					X	X		Smith 1959
Variable Seedeater *Sporaphila aurita*					X					Gross 1952
Cuban Grassquit *Tiaris canora*		X					X			Baptista 1978
Gray Catbird *Dumetella carolinensis*			X							Palmer 1949
Mockingbird *Mimus polyglottos*						X				Armstrong 1963
Brown Thrasher *Toxostoma rufum*		X	X	X						Thomas 1952
European Robin *Erithacus rubecula*						X				Lack 1939, 1943
Eastern Bluebird *Sialia sialis*								X		Thomas 1946
Russet Nightingale Thrush *Catharus occidentalis*		X		X	X					Skutch 1958
Gray-cheeked Thrush *Catharus minimus*							X	X		Van Tyne and Berger 1976
European Blackbird *Turdus merula*					X					Messmer and Messmer 1956
American Robin *Turdus migratorius*						X				Armstrong 1963
Brown Towhee *Pipilo fuscus*							X	X		Marshall 1960

TABLE 1. Continued.

Species	Situations in which female sings[a]					Suggested function(s)[a]				Source
	NB	NR	I	B	FY	TD	PB-M	C	F-GM	
Abert's Towhee *Pipilo aberti*							X	X		Marshall 1960
Orange-billed Sparrow *Arremon aurantiirostris*			X							Skutch 1954
Rose-breasted Grosbeak *Pheucticus ludovicianus*	X	X	X	X						Ivor 1944, Dunham 1964
Northern Cardinal *Cardinalis cardinalis*			X	X		X	X	X		Laskey 1944
Common Grackle *Quiscalus quiscula*							X			Wiley 1976
Greenfinch *Carduelis chloris*					X					Ferguson-Lees 1943
American Goldfinch *Carduelis tristis*	X									Berger 1953
Lawrence's Goldfinch *Carduelis lawrencei*	X									Linsdale 1950
Red Crossbill *Loxia curvirostra*							X			Lawrence 1949
White-winged Crossbill *Loxia leucoptera*								X		Bent 1968
Magpie Lark *Grallina cyanoleuca*							X	X		Robinson 1949
Butcherbird *Cracticus* sp.						X				Robinson 1949
Black-backed Magpie *Gymnorhina tibicen*						X				Robinson 1949

[a] NB = nest-building; NR = nest-relief; I = incubation; B = brooding; FY = feeding young; TD = territorial defense; PB-M = pair-bond maintenance; C = courtship; F-GM = family-group maintenance.

cording. During this period the situations in which females sang were noted, and hypotheses concerning the function(s) of this song were derived. During the second year of the study, these hypotheses were tested experimentally.

SYNOPSIS OF THE BLACK-HEADED GROSBEAK BREEDING CYCLE

The first birds arrived in the study area (Malibu-Guinavah Campground, in Cache National Forest 10 km east of Logan, Cache County, Utah) about the first week in May. Observations indicated that some birds were paired upon arrival. Such pairs may have been formed on the wintering grounds or during migration. During the early part of the breeding season, paired birds foraged together within their territories. The female usually followed the male as he moved through the territory feeding and singing. Such singing apparently serves a territorial function and, in addition, probably enables the female to maintain contact with the male. Females infrequently sang while foraging near the male (Weston 1947, pers. obs.).

Singing, alone, is not sufficient to maintain a territory, at least early in the breeding season, and agonistic encounters involving chasing and even physical contact occurred. Nearly all chases involved males, although several female-female chases were observed, and, on three occasions, females were observed chasing males. On one of these occasions, a female was observed chasing a male, and, upon landing, she sang one loud song. On another occasion a female appeared to engage in a brief singing duel with a neighboring male.

Following territory establishment, Black-headed Grosbeaks become progressively less aggressive. This change in behavior was quantified in two ways: (1) male singing rates de-

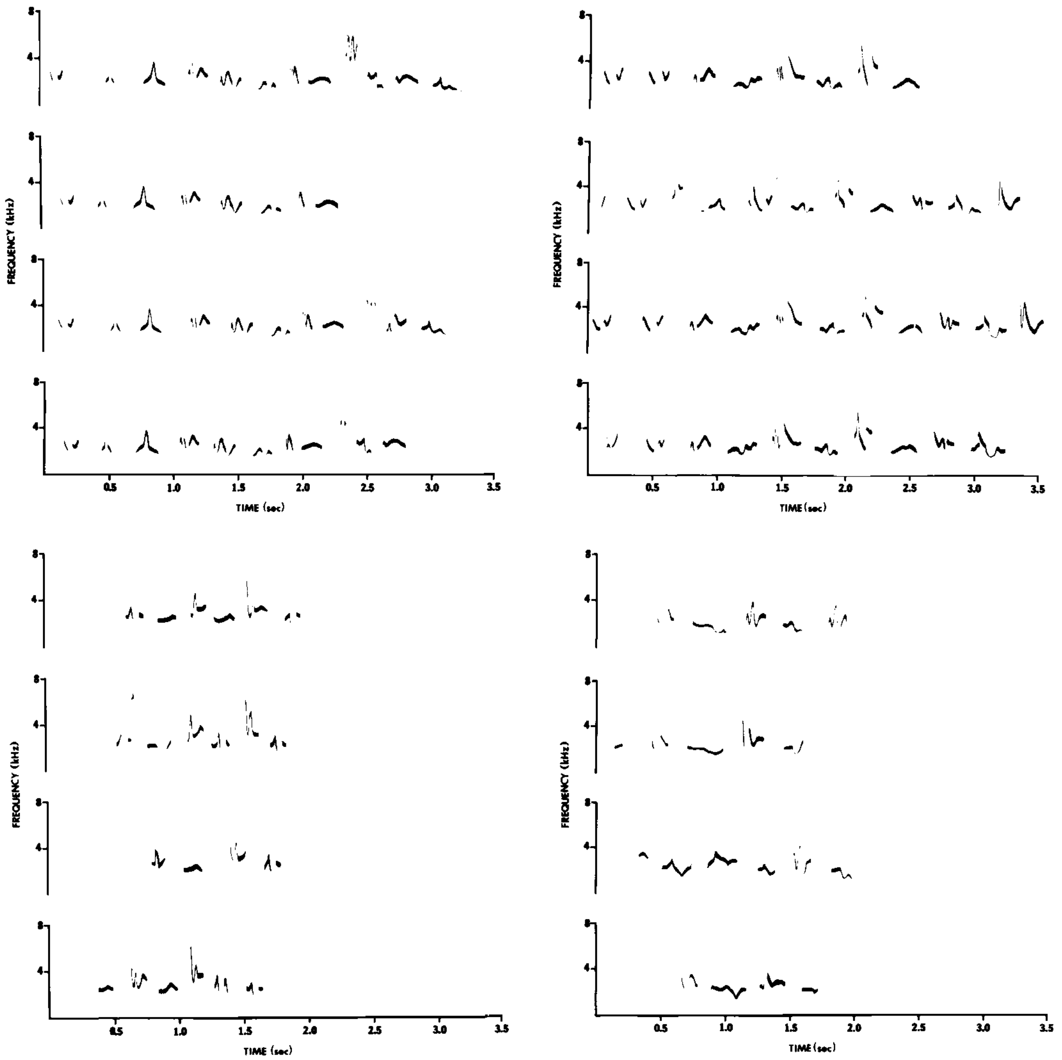

Fig. 1. Representative sonograms of the songs of male (above) and female (below) Black-headed Grosbeaks.

clined as the season progressed, and (2) the frequency of intraspecific agonistic encounters (i.e. chases and/or actual physical encounters) decreased (Fig. 2).

Nest building.—The female normally builds the nest, and I observed three instances in which females sang while involved in such construction. Twice, females sang while gathering nest materials, and, on another occasion, a female was observed singing while sitting in a partially constructed nest. On each of these occasions a male was within a few meters of the singing female.

Incubation.—Both sexes are surprisingly vocal on and around the nest. Males frequently sang while incubating. At times this song appeared to be in response to the singing of neighboring males, i.e. a male would be quietly incubating when, upon hearing a neighboring male singing, the incubating bird began to sing. At other times the male's singing appeared to be a signal to the female that he was about to leave the nest.

Females rarely sing while incubating. On two occasions incubating females sang in apparent response to the singing of neighboring males.

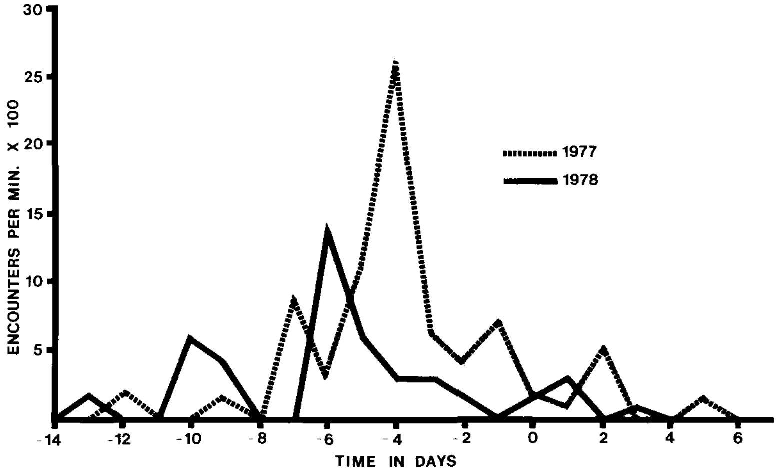

Fig. 2. Distribution of intraspecific agonistic encounters (chases and/or actual physical encounters) among male and female Black-headed Grosbeaks (Day 0 = first egg laid).

In most cases, however, females showed no response to the singing of neighboring males.

On many occasions a male or female would approach the nest and find its mate quietly incubating. At these times, males and females frequently uttered "chip" calls or sang. The incubating bird, upon hearing its mate, would then leave the nest.

Parental care.—During the first few days post-hatching, the adults maintained the same schedule as when incubating. Both adults fed and brooded the young, and their behavior when changing places on the nest was similar to that during incubation, with one significant difference. As the brooding period progressed, the females began to sing more frequently (Fig. 3).

By the eighth day post-hatching the young

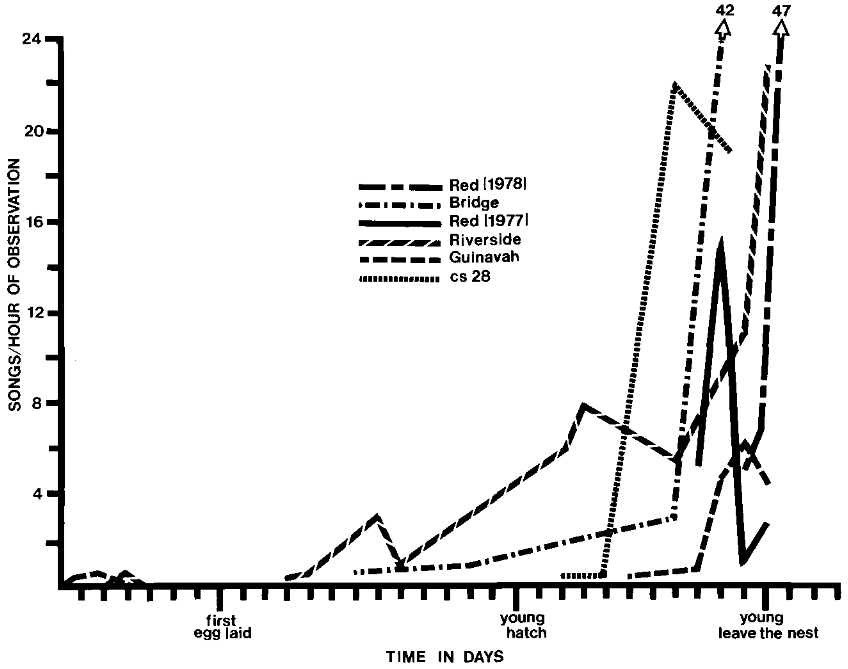

Fig. 3. Singing rates of selected females during the 1977 and 1978 breeding seasons.

were brooded infrequently. Adults approaching the nest to feed the young frequently vocalized. These vocalizations were either "chip" calls or songs. Upon the arrival of the adult at the nest, the young grosbeaks immediately began calling. At times the young began calling upon hearing the calls or songs of their parents.

The young may leave the nest as early as the ninth day post-hatching, although departure at 10–14 days post-hatching was more common ($n = 21$, $\bar{x} = 11.5$). After leaving the nest they scatter among the shrubs near the nest, perching on low branches. During the first few days, the young are rather quiet. As they are unable to fly at this time, they remain within a restricted area, and the adults generally have little trouble locating and feeding them (Weston 1947, pers. obs.). If, however, a parent is unable to locate a young bird, the parent will begin to utter "chip" calls and/or songs. Upon hearing their parents' vocalizations, young grosbeaks respond by uttering "phee-oo" and/or "hunger-distress" calls. In this manner the parents and young are able to maintain contact.

Maintaining contact between the parents and their young obviously becomes more difficult after the young attain flight (approximately 15 days post-hatching). To maintain contact, grosbeaks appear to use the same system described above. When parents have food for the young, but are unsure of the location of the young, the parents begin to utter "chip" calls or, more frequently, songs. Upon hearing a parent, young grosbeaks utter "phee-oo" and/or "hunger-distress" calls. The parent then flies to the young bird and feeds it. Occasionally, after hearing a parent sing, a young grosbeak will fly to within a few meters or less of the adult and, if not fed immediately, will begin calling.

At this stage (2–3 weeks post-hatching), family groups begin to wander and no longer stay within their territories. Because of this wandering, it is difficult to observe specific family groups over long periods, and, therefore, the duration of such groups remains a question. Weston (1947) reported seeing young grosbeaks being fed by adults in early August, but he was unable to determine the actual length of the dependent period.

Summarizing the above observations, I found that both male and female Black-headed Grosbeaks sing in the following situations: (1) as they forage with their mates before nesting, (2) after chasing neighboring males from their territory, (3) during nest building, (4) during incubation, (5) during change-overs at the nest (both during incubation and brooding), (6) when coming to the nest to feed the young, (7) when attempting to locate and feed fledged young.

These observations, along with those of Head (1902, 1904) and Weston (1947), suggested the following generalized functions of female song in the Black-headed Grosbeak: (1) maintenance of the pair bond, (2) territorial defense, (3) family-group maintenance.

Other reports (Ritchison in prep.) have revealed that female song in the Black-headed Grosbeak does appear to be important in the maintenance of the pair bond, although it plays no role in territorial defense. The main objective of the present study was to examine the possible role of singing by female Black-headed Grosbeaks in family-group maintenance.

MATERIALS AND METHODS

Fieldwork was conducted during the breeding season of 1978 at Malibu-Guinavah Campground. Eight young grosbeaks from five different nests were tested in these experiments. All birds tested were between 10 and 17 days of age.

Apparatus.—Testing was conducted in an automobile from which the birds had no contact (visual or vocal) with their parents or other grosbeaks. The test apparatus consisted of a testing arena and a portable tape recorder (Nagra IIIB) connected by cable to a portable loudspeaker.

The arena was a box with floor dimensions of 125 × 28.8 cm and walls 28.8 cm high. The floor and long walls of the box were made of wood while the short walls consisted of cheesecloth. To provide a reference grid for the purpose of scoring a bird's position in the arena, the floor was marked out into 25 5-cm cells. In addition, the top of the apparatus was covered with a wire screen.

During tests the observer sat in the front seat of the automobile and viewed the floor of the arena by means of a mirror suspended at an angle above it. For the playback of recorded songs the portable loudspeaker was placed against the cheesecloth at one end or the other of the arena, and the tape recorder was controlled by the observer from the front seat.

Playback recordings.—The songs of parents and strangers were recorded using a Nagra IIIB tape recorder with an Altec 633A microphone, which was housed in a 62-cm parabolic reflector. All recordings were made at a tape speed of 19 cm/s (7½ ips). From these recordings were made 3-min test tapes, with songs spaced at 15-s intervals.

Testing procedure.—Each bird was tested alone. Initially, the young bird was placed at the central position on the floor grid of the arena, and its behavior during the next 3 min was observed and scored without playback of any sound through the speaker. Such a period will be referred to as a "pre-test." At the end of a pre-test, the young grosbeak was replaced at the central position of the floor grid. For the next 3 min songs were played, and again the behavior of the bird was observed and scored. Such a period with playback will be referred to as a "test." Immediately after the test period, the young bird was again replaced at the central position of the floor grid. Its behavior during the next 3 min was again observed and scored. Such a period without playback after the test period will be referred to as a "post-test."

Each bird was exposed to four types of test in this way: two parental tests, in which the songs of its mother and father were played, and two "stranger" tests, in which the songs of strange males and females were played. The young birds experienced each of the four types of pre-test/test/post-test sequences twice, once with the speaker at one end of the arena and once with the speaker at the other end. The sequence of presentation was either parental-stranger-parental-stranger or stranger-parental-stranger-parental; as many birds experienced the one as the other. The sequence in which the ends of the arena were used was also varied among birds, and the order of ends was independent of the order of test types. The complete sequence of testing for a young grosbeak thus consisted of 8 pre-test/test/post-test runs, each 9 min in duration. I allowed 5 min between each run for rewinding and changing test tapes on the tape recorder. The young bird remained in the arena during this time.

For the tests the volume controls of the tape recorder were adjusted so that modulometer readings were similar for each tape used. No precise measurements of sound intensity levels in the arena were made, however.

Scoring.—For the purposes of scoring the behavior of the young grosbeaks, each pre-test, test, and post-test was divided into 12 15-s intervals. At the end of each 15-s interval, a bird's position, orientation, and the types and numbers of calls were noted. Details of the conventions used for scoring the behavior of the young grosbeaks are as follows:

(i) Orientation. Two scores for orientation were accumulated: one for orientation toward the speaker end of the arena and one for orientation toward the other end. A bird was judged as oriented to one end or the other if it was pointed directly toward that end or in a direction within 20° to either side of the direct line from it to the end. In each 15-s interval the bird was thus scored as oriented toward the speaker end, or as oriented toward the other end, or as unoriented. By counting up the intervals in which orientation was one way and the intervals in which it was the other way I obtained the two scores. In a 3-min pre-test, test, or post-test, therefore, the maximum possible score for one end, and for the two ends taken together, was 12.

(ii) Position. As in the procedure for orientation, two scores were obtained: one for the speaker end of the arena and one for the other end. The central position in the arena, from which a bird started out in each pre-test, test, and post-test, carried a position value of 0. The 5-cm transverse divisions of the floor carried position values, which increased from 1 to 12, reading from the central position to one side or the other. At the end of each 15-s interval, a bird's position on the floor grid, determined by the location of its feet, was noted and scored. Summing the scores for the two sides separately gave the two position scores. The maximum possible score in a 3-min pre-test, test, or post-test, for one side or for the two sides taken together, was therefore 144 (12 × 12). The maximum score would result if a bird spent all 12 intervals of a pre-test, test, or post-test within 5-cm of one or other of the end-walls of the arena.

(iii) Position Change. A 15-s interval was scored as positive for position change if the bird's position on the floor grid at the end of that interval was different from what it had been at the end of the preceding interval, regardless of direction. The maximum score for position change in a 3-min pre-test, test, or post-test was therefore 12.

(iv) Calling. The types and numbers of calls given by a bird during the pre-test, test, and post-test periods were noted.

Playback experiments with free-living young.—In addition to tests in the apparatus, a series of experiments were performed with young grosbeaks in a natural setting, i.e. while the birds were perched in a bush or small tree. Each experiment consisted of three 5-min segments (pre-test, test, post-test), and throughout each test all sounds and nonvocal behavior were noted. Each bird was tested twice with its mother's songs, and trials were at least 1 day apart. The speaker was placed 5–10 m from the young grosbeaks in these experiments.

Playback experiments with adult females.—The responses of females to playback of the "phee-oo" calls of their young were also examined in the field. The procedures followed in these tests were the same as those used in the playback experiments with the young. Each experiment consisted of three 5-min segments (pre-test, test, and post-test). Throughout each test all sounds and non-vocal behavior were noted. Each female was tested twice with the "phee-oo" calls of one of her young. Different trials were at least 1 day apart.

TABLE 2. Responses of young grosbeaks to playback of female song in the test apparatus.

	Mean scores[a,c]						Significance levels[b,c]				
	PPT	SPT	PT	ST	PAT	SAT	PPT vs. SPT	SPT vs. ST	PPT vs. PT	PT vs. ST	PAT vs. SAT
Orientation to speaker	2.4	1.7	5.4	2.4	5.1	2.5	NS	NS	NS	0.05	NS
Orientation to other end	1.3	1.9	1.3	2.0	1.2	2.8	NS	NS	NS	NS	NS
Position score, speaker end	18.1	8.6	33.6	17.9	13.5	17.0	NS	NS	NS	NS	NS
Position score, other end	31.0	37.1	28.8	32.4	32.0	25.0	NS	NS	NS	NS	NS
Position change	2.2	4.5	2.4	2.0	0.6	1.2	NS	NS	0.02	0.02	NS
Number of "phee-oo" calls	17.4	15.7	54.2	27.0	37.6	26.8	NS	0.05	0.01	0.01	0.05
Number of "hunger-distress" calls	0.3	0.3	10.5	2.2	0	0	NS	NS	0.01	0.02	NS

[a] The mean scores were derived from two sets of experiments on each of eight birds. The significance levels are according to Wilcoxon matched-pairs tests, two-tailed.

[b] $P <$ number given: NS = not significant.

[c] PPT = parental pre-test; SPT = stranger pre-test; PT = parental test; ST = stranger test; PAT = parental post-test; SAT = stranger post-test.

RESULTS

Responses of young grosbeaks to parental song in the test apparatus.—The results are summarized in Tables 2 and 3, together with significance levels, given by Wilcoxon comparisons, for the differences among all pre-tests, tests, and post-tests. As these figures and comparisons clearly show, the young grosbeaks moved about more, called more, and were more often oriented toward the speaker in response to parental song than to the songs of strangers. The effects on a young grosbeak's behavior of playing the parental songs were spectacular in most cases. Typically a bird's behavior in the pre-tests consisted of standing or sitting near the center of the arena and giving occasional "phee-oo" calls. At the sound of the parental song, however, there was usually an immediate and sudden change: the young grosbeak raised its head and started calling (often beginning by uttering a series of "hunger-distress" calls followed by nearly continuous "phee-oo" calls). In general, then, there was incessant calling and locomotion (i.e. position change) in the parental tests.

Responses of young grosbeaks to the songs of strangers in the test apparatus.—Although the responses of the young grosbeaks to playback of the songs of strangers were less pronounced, they were still significant in several categories of response (Tables 2, 3). As in the parental tests, the young grosbeaks' first response to the songs of strangers was often a series of "hunger-distress" calls followed by nearly continuous "phee-oo" calls. This vocal response to the songs of strangers, however, was significantly less pronounced than the response to parental song (Tables 2, 3). In addition, strangers' songs elicited no significant locomotory responses. Finally, young grosbeaks showed a significant orientation away from the speaker in response to the playback of the songs of strange males (Table 3).

Playback experiments with free-living young.—In the test apparatus, as well as under natural conditions, young grosbeaks responded to parental song by uttering "phee-oo" calls and/or "hunger-distress" calls. A comparison of the responses of young birds in the apparatus and in a natural setting, however, revealed differences with respect to orientation and approach. Under natural conditions young grosbeaks showed a significant tendency to approach the speaker (Table 4); birds in the test apparatus, however, showed no such tendency (Tables 2 and 3). Young grosbeaks in the apparatus did, however, show increased locomotion. These results, although not predicted initially, might be explained as follows. In precocial species, such as the Laughing Gull (*Larus atricilla*; Beer 1970a, b) and Ring-billed Gull

TABLE 3. Responses of young grosbeaks to playback of male song in the test apparatus.

	Mean scores[a,b]						Significance levels[a,b]				
	PPT	SPT	PT	ST	PAT	SAT	PPT vs. SPT	SPT vs. ST	PPT vs. PT	PT vs. ST	PAT vs. SAT
Orientation to speaker	2.8	2.4	3.2	1.5	2.3	2.4	NS	NS	NS	0.05	NS
Orientation to other end	1.5	1.8	2.1	3.4	2.5	2.4	NS	0.02	NS	NS	NS
Position score, speaker end	13.1	11.8	18.2	11.5	27.2	31.9	NS	NS	NS	NS	NS
Position score, other end	12.3	23.6	37.0	36.4	19.8	36.6	NS	NS	NS	NS	NS
Position change	0.6	0.7	5.2	1.7	1.7	1.1	NS	NS	0.01	0.01	NS
Number of "phee-oo" calls	17.9	23.0	62.9	44.1	37.4	28.7	NS	0.01	0.01	0.01	0.01
Number of "hunger-distress" calls	0	0.1	7.9	9.3	2.7	0	NS	0.02	0.02	NS	NS

[a] Mean scores and significance levels as in Table 2.
[b] PPT = parental pre-test; SPT = stranger pre-test; PT = parental test; ST = stranger test; PAT = parental post-test; SAT = stranger post-test.

(*L. delawarensis*; Evans 1970b), chicks have been found to show orientation and approach responses to the played-back calls of their parents. Because precocial chicks normally approach their parents by walking or running, the quickest route to a "calling parent" (i.e. the speaker) is to orient toward and approach the sound source. In the grosbeak, on the other hand, young birds come in contact with their parents by flying toward them or, if they are not yet capable of flight, by remaining motionless and calling the adults toward them. In the apparatus, therefore, young grosbeaks would not be expected to walk or run toward the sound source (speaker), but instead (depending on the age of the young) would either remain motionless and call or attempt to "fly" out of the apparatus to locate and approach their unseen parent. Such reasoning might explain the absence of significant orientation or approach behavior by young grosbeaks in the test apparatus.

Playback experiments with adult females.—The responses of females to the playback of the begging calls ("phee-oo" calls) of their young were significant in several categories, i.e. distance of closest approach, number of songs, and syllables per song (Table 5). Because only the calls of their own young were played to individual females, these results do not constitute proof of individual vocal recognition of young by females. As will be discussed later, how-

TABLE 4. Responses of free-living young Black-headed Grosbeaks to playback of their mother's song.

	Closest approach (m)	Number of flights	Number of "phee-oos"	Number of "hunger-distress"	Number of "chips"
Responses[a]					
Pre-test period (PTP)	7.00	0	0.20	0	0.10
Test period (P)	3.30	0.80	2.50	1.60	0.40
Post-test period (PP)	3.50	0.30	0	0	0.30
Significance levels[b]					
PTP vs. P	0.05	0.05	0.05	NS	0.05
PTP vs. PP	0.05	NS	NS	NS	0.05
P vs. PP	NS	0.05	0.05	NS	NS

[a] Values for responses are averages for all tests. The significance levels are according to paired t-tests ($n = 6$).
[b] $P <$ number given; NS = not significant.

TABLE 5. Responses of females to playback of the "phee-oo" calls of their young.

	Closest approach (m)	Number of songs	Syllables per song	Number of "chips"	Number of "wheets"	Number of "distress"	Number of flights
Responses[a]							
Pre-test period (PTP)	7.00	0	0	5.70	0	0	5.70
Test period (P)	3.00	1.70	5.60	23.20	10.40	0.20	7.20
Post-test period (PP)	4.80	3.80	4.70	13.90	1.20	0	3.20
Significance levels[b]							
PTP vs. P	0.01	NS	NS	0.05	NS	NS	NS
PTP vs. PP	0.05	0.05	0.001	NS	NS	NS	NS
P vs. PP	0.05	0.05	0.05	NS	NS	NS	0.01

[a] Values for response are averages for all tests. The significance levels are according to paired t-tests ($n = 4$).
[b] $P <$ number given; NS = not significant.

ever, these results do lend support to the conclusion that singing by females is important in family-group maintenance.

DISCUSSION

Recent studies involving the recognition of parents by their young have concentrated on colonial species, e.g. Common Murres (*Uria aalge*; Tschanz 1965, 1968), Black-billed Gulls (*Larus bulleri*; Evans 1970a), Laughing Gulls (Beer 1970a, b), Ring-billed Gulls (Evans 1970b), and Black-Legged Kittiwakes (*Rissa tridactyla*; Cullen 1957). Evidence of individual recognition between parents and young has been found in every colonial species in which it has been sought, with the exception of the Black-legged Kittiwake. The survival value of this recognition in colonial species seems quite apparent. Because a young bird is surrounded by adults who are not its parents, who are unlikely to feed it, and who may even attack it, individuals who beg only from their own parents should conserve energy and have a selective advantage over indiscriminating young. The case of the Black-legged Kittiwake may be regarded as an exception that proves this rule, for in that species the young remain confined to the nest until they fledge (Cullen 1957), so that up to that time the young do not normally encounter adults other than their parents.

In contrast to the situation described for colonial species, there is little information available concerning the recognition of parents by their young in noncolonial, altricial species. Only a few observations suggesting the possibility of such recognition have been reported. For example, Michener and Michener (1935) stated that a young Mockingbird (*Mimus polyglottos*) recognized the voice of the parent who fed it and started to beg on hearing it. Nestling European Blackbirds (*Turdus merula*) are reported to know their mother by her food call (Messmer and Messmer 1956), and fledged young apparently recognize their fathers' vocalizations (Thielcke-Poltz and Thielcke 1960). Young Ring Doves (*Streptopelia risoria*) and Chiffchaffs (*Phylloscopus collybita*) are also reported to recognize the calls of their mother (Craig 1908, Gwinner 1961). Other authors have reported observations suggesting that altricial young may recognize parental song. For example, Saunders (1929) referred to young House Wrens (*Troglodytes aedon*) being stimulated to open their bills by the males' song. Young Snow Buntings (*Plectrophenax nivalis*) may also be able to distinguish their father's song from the song of other males (Armstrong 1963). The present study provides clear evidence that young Black-headed Grosbeaks are able to recognize the songs of their parents.

Grosbeak family groups begin to wander 2–3 weeks after hatching and no longer stay within their breeding territories. Because the birds are moving through thick vegetation in unfamiliar areas, maintaining contact becomes more difficult. Under such conditions individual vocal recognition is essential. Without such recognition, the maintenance of family groups would probably be impossible. The need for the recognition of parental song by young grosbeaks, therefore, is apparent. Even with such recognition, however, it would certainly be possible for young grosbeaks to stray from the family groups. Given that possibility, a positive response to the songs of other adult grosbeaks would be advantageous. Such a response to strange adults would presumably tend to enhance the chances of "adoption" by foster parents. This, in fact, appears to be the "strategy" used by young grosbeaks. Although fledglings respond more strongly to the songs of their own parents, they also show significant responses to the songs of strange males and females (Tables 2, 3).

The responses of young grosbeaks to parental song represent but one side of the parent-young relationship. The responses of parents to the vocalizations (or absence of vocalizations) of their young are equally important. Among older fledglings, contact with parents generally results from these fledglings flying to the parents in response to parental song. Younger fledglings, however, as well as young birds that have left the nest but are not yet capable of flight, maintain contact with parents by means of the mutual recognition system discussed previously, i.e. an adult with a food item, but unaware of the location of its young, will often begin singing to elicit begging ("phee-oo" and/or "hunger-distress" calls) from its young. In this way a parent is able to locate its young. The responses of females to the playback of the "phee-oo" calls of their young appear to verify the existence of such a system. Upon hearing the playback, females showed a significant approach response, as well as significant increases in the number of flights and number of "chip" calls (Table 5). Such responses would, under natural conditions, enable a parent to locate a young grosbeak quickly. On the other hand, once playback ended, females showed significant increases in singing rates. Under natural conditions this would elicit calling by young grosbeaks and, thus, allow a parent to locate its offspring.

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NOTES ON THE BEHAVIOR OF THE COSTA RICAN SHARPBILL (*OXYRUNCUS CRISTATUS FRATER*)

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ABSTRACT.—The Costa Rican Sharpbill (*Oxyruncus cristatus frater*) is a chunky bird of stolid demeanor, with rapid and jerky movements. Males apparently form exploded leks of 3–4 birds, advertising their lek territories by singing a high, thin, wiry, descending trill from conspicuous perches high in the canopy of precipitous, mid-elevation rain forest. The singing (and probable breeding) season extends from late February or March to late May or early June. The bright vermilion crest of the males is erected during intense aggressive interactions but not during singing. Probable courtship is described, but we were unable to observe copulation. We also describe a probable flight display of unknown significance. Sharpbills employ varied foraging tactics and take both fruit and animal prey. The sharp-pointed bill is used to pry open rolled leaves, undehisced fruits, and tufts of moss and epiphytes. The Sharpbills' bill and foraging appear to represent a unique specialization within the great tyrannine suboscine radiation of the New World tropics and a striking convergence with the family Icteridae in particular. *Received 18 January 1982, accepted 31 August 1982.*

THE Sharpbill (*Oxyruncus cristatus*) is a wide-ranging but extremely poorly known suboscine, generally placed in its own monotypic family. Five apparently disjunct races have been described over its broad distribution from Costa Rica to Paraguay, with the peculiarity that the northernmost and southernmost forms are more similar to each other than either is to the intervening forms (Chapman 1939). The northernmost race, *O. c. frater* Sclater and Salvin, has been recorded from Bijagua, in the Cordillera de Guanacaste of northern Costa Rica, south to Veraguas, Panamá, principally on the Caribbean slope but with one specimen each from San José and Santa María de Dota, on the Pacific slope (Slud 1964, Wetmore 1972). From specimen records and his two observations of the bird in Costa Rica, Slud (1964) considered it a bird of heavily forested regions in the cool and very humid portions of the subtropical belt, where it occurred in the canopy and in tall trees at the forest border. He noted it foraging in dense foliage at medium heights in the trees, clinging upside-down while feeding on small berries. We know of no other substantive published accounts of *O. c. frater* in life, and there are very few of any of the other races. Wetmore (1972) describes the body proportions, pterylography, and stomach contents of two *O. c. brooksi* he collected in Darién, Panamá, while E. Eisenmann (cited in Ridgely 1976) ascribes to *O. c. cristatus* of Brazil "a long-drawn high thin whistle that gradually slides down in pitch." Also, we have recently received a short account by T. H. Davis of the behavior of *O. c. hypoglauca* of Suriname (in litt.), which will be discussed below in connection with our observations of *O. c. frater*.

In this paper we describe the song, singing behavior, and probable social system of *O. c. frater*, including a flight display and a possible courtship vocalization. We also present observations on foraging and other behaviors, some of which appear to shed light on the species' chief morphological peculiarity, its sharp-pointed bill. Our observations of Sharpbills were made in Parque Nacional Braulio Carrillo, Provincia de San José, Costa Rica, chiefly in the vicinity of "La Montura," a house beside the road (under construction) from San José to Guápiles, in the Atlantic lowlands. Except for a narrow strip of devastation along the road itself, the area is heavily forested; the terrain is exceedingly precipitous (see Fig. 3). Most observations were made at an elevation of about 1,100 m, near the top of a steep-sided ridge that separates the Río Patria watershed on the west from that of the Río La Hondura to the east. The general area falls in the Premontane Rain Forest life zone of Holdridge (1967). Between

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late June 1980 and early April 1982, Stiles made a total of 18 visits of 1–5 days' duration to La Montura, accumulating some 18 h of observations on singing Sharpbills plus numerous observations on foraging and other behaviors. Whitney watched singing Sharpbills for about 8 h on 17–18 March and 4 April 1982 at La Montura and briefly observed other behaviors there and elsewhere on the same dates.

GENERAL APPEARANCE AND BEHAVIOR

In life, Sharpbills appear chunky and short-legged, about the bulk of a kingbird (*Tyrannus*) but with a relatively smaller head and bill and a shorter tail (Fig. 1a). The upperparts are olive green, with two yellowish wingbars; the underparts are pale yellow, the breast and sides heavily spotted with black. The feathers of the head and throat are flecked or scaled with blackish. Those of the sides of the crown are tipped black (more broadly in males) and obscure a bright erectile median crownpatch, which in the male is bright vermilion, having more and longer feathers than the paler orange patch of the female and forming a conspicuous crest when fully erected. The iris of singing males appears reddish, the bill and feet grey; there may be a sexual difference in iris color, because a bird that visited a song perch of a male and was tolerated by him in the vicinity had an orange iris and was almost certainly a female (see below). The other notable sexual difference involves the outermost (tenth) primary: in males, but not females, the barbs of the basal two-thirds of the outer web are stiffened and recurved, giving a saw-toothed effect not unlike that of the outermost primary of male *Stelgidopteryx* swallows. Notwithstanding these differences, the sexes are too similar in appearance to be safely distinguished in the field under any but the most favorable circumstances.

Sharpbills usually perch erectly and rather stolidly, often sitting in the same spot for minutes at a time (although looking alertly about). When they do move, their movements are abrupt and jerky, with heavy hops and jumps in foliage or fast, direct flights between trees. The normal flight consists of bursts of fast, shallow wingbeats alternating with short level glides. The birds usually alight in dense foliage, where they may sit quietly or progress by short hops and flights upward and outward to the edge of the canopy. Even when perched in plain sight, Sharpbills are often difficult to observe, owing to their inconspicuous colors and sluggish demeanor. The Sharpbill's stolid manner was most evident on one of the few occasions when Stiles saw a male's crest (partly) raised. This occurred when a male flew from his song perch to join a furious aggregation of tanagers, honeycreepers, warblers, and hummingbirds that were responding by vigorous mobbing behavior to Stiles' whistled imitations of the call of the Highland Pygmy-Owl (*Glaucidium jardinii*). Flying rapidly into a nearby tree, the Sharpbill hopped swiftly up to a perch in dense foliage and sat for several minutes peering incessantly about, partly raising and lowering its crest several times. Its sluggishness contrasted strikingly with the active flitting of the other birds, its silence with their excited scolding.

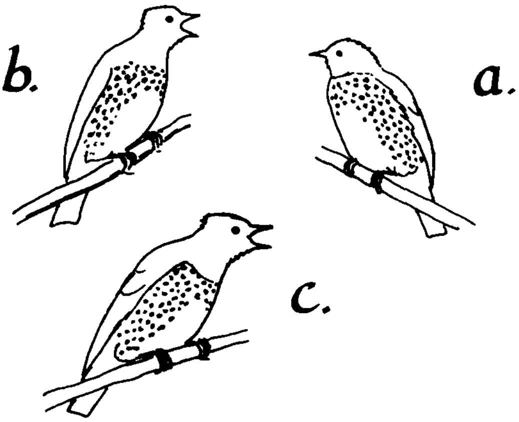

Fig. 1. Some postures of the Sharpbill, drawn from 35-mm slides. a. Normal perching posture. b. and c. Singing male.

Sharpbills are solitary birds under most circumstances. Singing males only exceptionally tolerate other individuals, probably females (see below), near their song perches. We have never seen any lasting association between two Sharpbills nor any indication that the singing areas of males are also nesting areas. In our experience, foraging Sharpbills are also seen singly, although they may associate loosely with mixed-species flocks, particularly those canopy flocks organized around parties of tanagers (*Chlorospingus ophthalmicus* and/or *Tangara* spp.). Sharpbills seem to join flocks that remain for some time in the same spot rather

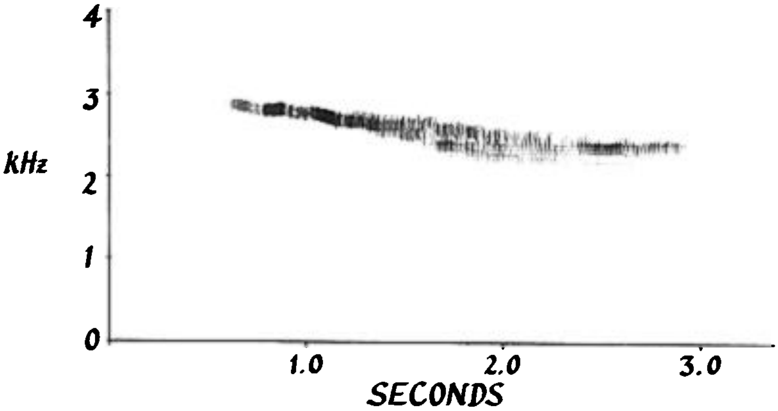

Fig. 2. Sonagram of the song of the Sharpbill, recorded 22 March 1981 on a Uher 4000-L recorder. Sonagram prepared by J. W. Hardy.

than moving with the flock for considerable periods. Davis (in litt.) reports that Sharpbills in Suriname regularly join and follow mixed-species foraging flocks.

SONG AND SINGING BEHAVIOR

The most conspicuous vocalization of the Sharpbill at La Montura is a high, thin, wiry, descending trill sounding like "eeeeuuuurrr," with a rather cicada-like quality. The sonagram (Fig. 2) shows the trill to have a duration of about 2.5 s; it commences at a frequency of about 3 kHz, descends to about 2.5 kHz, and has a fine structure of about 65 syllables/s. Vocalizing birds usually perch on dead or thinly foliaged branches projecting conspicuously out of the canopy, about 15–30 m above ground (Fig. 3). Each bird seems to use a small number (ca. 3–5) of such perches regularly, within a radius of 50–100 m; the calling areas of adjacent birds do not overlap, and in fact the birds appear to defend them (see below). The only vocalizing birds that we could observe closely definitely had the vermilion crown-patch of the male Sharpbill; because the behavior of all calling birds seemed similar, we conclude that all such birds were probably males. The loudness, stereotypy, and persistent delivery from conspicuous, defended perches of this vocalization convince us that it represents the territorial advertising song of the species. A similar vocalization was heard from Suriname Sharpbills by Davis (in litt.), who reached a similar conclusion regarding its function.

The singing season of the Sharpbill at La Montura is from late February or early March to late May or early June. In 1981, Stiles heard no Sharpbills singing on 8–9 February, but they were in full song by 13–15 March. In 1982, he heard only very sporadic singing on 17–19 February, but by 17–18 March Whitney found them in full song. Song was still frequent on 22–25 May 1981 but was not heard on 1–5 July (nor on 29 June–4 July 1980). The singing season is almost certainly synonymous with the breeding season, as nearly all small canopy-dwelling birds (except hummingbirds) at La Montura breed during these months (Stiles unpubl. data).

In both 1981 and 1982, the number of singing males at La Montura varied from 3 to 4 on different dates; their territories were arranged in a loose cluster on both sides of the ridgetop (Fig. 4). Most of our observations of song and social behavior were of the male whose territory included the ridgetop itself, hereafter called the "ridgetop male" (although in the absence of banded birds we cannot be certain that the same individual was involved in both years). The arrangement of territories varied somewhat between years, although many of the same song perches were used in both (evidently sometimes by different males). In 1982, a dead treetop some 40 m northeast and slightly below the house was a regular song perch of the ridgetop male and proved exceptionally favorable for observation; most of the significant social interactions seen involved this perch and its vicinity. (In 1981 this tree was alive, bore thick foliage, and was not used as a song perch.) No other singing Sharpbills were located in the

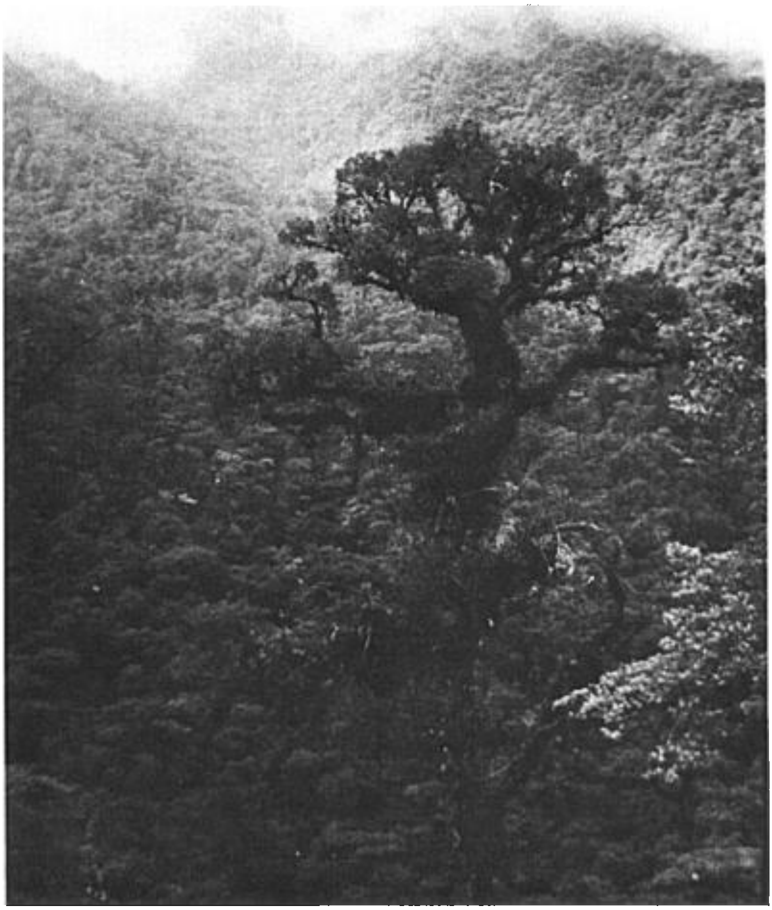

Fig. 3. Forest at La Montura, including two song perches of the ridgetop male (1981): the dead branch in the extreme upper left of the large (ca. 25-m) tree at center, and the uppermost diagonal branch of the smaller (ca. 17-m), thinly foliaged tree at the extreme right. Photo taken looking southwest across the road into the Río Patria drainage; note the steepness of the terrain and the quantity of moss and epiphytes in the large tree at center.

La Montura area, despite repeated visual and auditory searches along several kilometers of roadside and study trails.

The singing posture of the perched bird was characteristic: it stretched its neck forward, fluffing its head feathers and opening its bill wide (Fig. 1b, c). The vermilion crown-patch was never exposed during singing; indeed, the feathers often appeared so tightly appressed as to form a concavity in the center of the crown. During periods of active singing, the ridgetop male gave an average of about two songs per minute (interval between songs 15–58 s, mean 31 s for 17 successive songs at about 1300 on

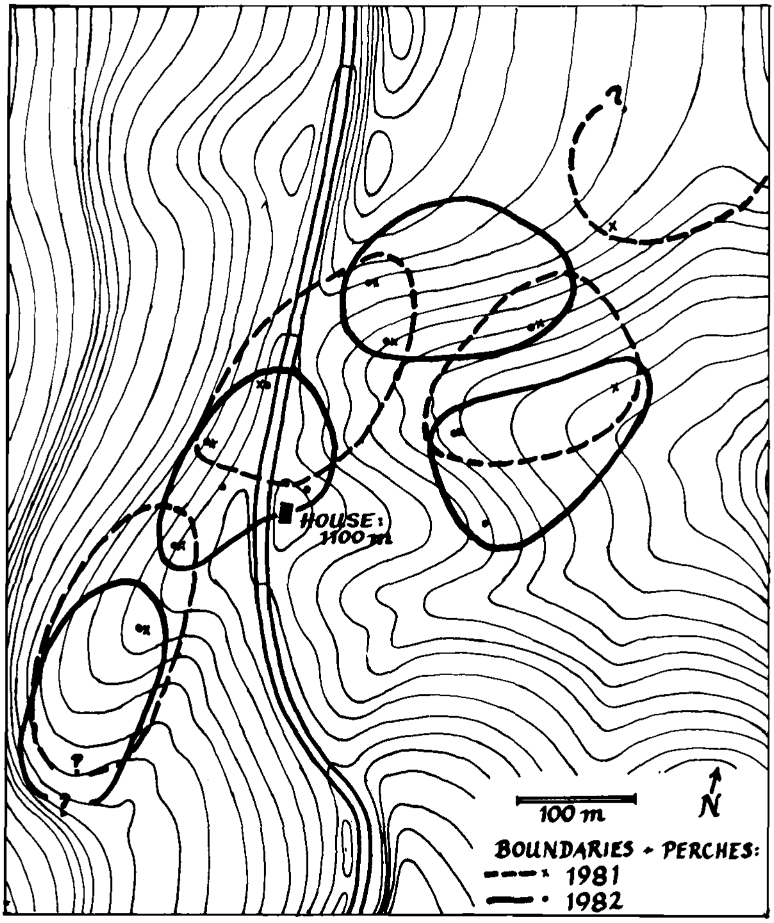

Fig. 4. Approximate locations of territories and song perches of Sharpbills at La Montura in 1981 and 1982. Contour interval about 10 m; note extreme steepness of terrain.

21 March 1981). A typical song bout contained about 10 songs (mean 10.7, range 3–21 for 11 bouts on 21 March and 16 April 1981); generally, the ridgetop male changed perches one or more times during a song bout (mean number of consecutive songs from a perch 3.8, range 1–9 for 8 bouts on 16 April 1981). About 10% of the songs were given from perches other than the regular song perches (in the case of the ridgetop male, many songs were given from two *Clusia* feeding trees immediately behind the house). Often the ridgetop male was answered by, or sang in response to, other singing males on either side of the ridge. During the height of the singing season, the Sharpbills sang most consistently around midday (ca. 1000–1400). During clear weather, the ridgetop male spent 40–80% of his time on his song perches during these hours and foraged largely within sight of them. Even at these times, however, he was often absent for 5–15 min at a stretch. A briefer and less intense period of singing usually occurred at 0540–0700; during the rest of the day, singing was highly sporadic. Periods of heavy rain often disrupted this schedule; during the very rainy observation period of April 1981, the birds did not sing at all on some days.

The only instance in which markedly different singing behavior was observed occurred at about 1530 on 4 April 1982, some 8 km north of La Montura, at an elevation of about 700 m. Whitney observed a lone Sharpbill perched on a small dead limb near the top of a tall (ca. 20 m) tree at the edge of a clearing. This bird's song seemed slightly higher-pitched, thinner, and shorter than the songs of the La Montura birds but was easily recognizable as that of a Sharpbill. After giving a song, the bird sat silently on its perch for 3–4 min, then suddenly launched into a strange, rapid, fluttery flight in which the wings quivered while the tail pumped sharply downward as the bird flew directly across the clearing. While in mid-flight, the bird jerked its head up slightly, opened its bill wide, delivered one song, and continued flying until lost from view behind a tree, after which it could not be relocated. The song given in flight sounded exactly like that which the bird had just given from a perch. No possible mechanically produced sounds were heard during this peculiar flight, so the function of the serrations of the male's outer primary remains unknown. We have never seen such a flight display at La Montura and cannot divine its significance at present. Whitney found no other Sharpbills in this area, nor had either Stiles or Whitney seen or heard any in several visits during the 1981 singing season. Unfortunately, a landslide blocked access to this area in May 1982.

AGGRESSIVE AND COURTSHIP BEHAVIOR

We rarely saw a male on his song perch interacting closely with another Sharpbill and estimate that the ridgetop male on his song perches was quite alone for at least 95–98% of the time. On several occasions Stiles saw this male give what appeared to be a stylized double wing-stretch, snapping his wings half open horizontally, holding the pose for a second or so, then snapping them shut. Such movements occurred more often during a bout of singing back and forth with another male, but Stiles was unable to determine whether or not the males were in visual contact. Certainly no other Sharpbill was detected close to the male's song perch on such occasions, and we do not know the function (if any) of this apparent display.

Nevertheless, two types of social interactions centered about the males' song perches were observed: aggressive interactions, evidently involving two males, and what appeared to be female visits leading to courtship. At least some of the departures of the ridgetop male from his territory were evidently for the purpose of interacting with other males. At about 1130 on 21 March 1981, some 2 min after this male had flown east down the hill toward another singing male, Stiles saw two Sharpbills burst out of a tree some 75 m below the road, locked in combat. The fluttering, grappling birds dropped about 10 m and separated; one flew off to the east, and the other, evidently the ridgetop male, flew to a tree just below the road and perched, his crown-patch fully erected into a flaming crest. He gradually lowered his crest and after a minute or so began to sing while hopping about in dense foliage. Finally, he flew to one of his regular song perches and sang for several minutes, during which time he was answered several times by the bird to the east. On three other occasions, Stiles saw another Sharpbill fly in and land near the song perch of the ridgetop male, who without further ado launched himselt at the intruder and chased it out of sight. Twice he remained out of contact for several minutes, but after one such incident on 18 February 1982 he returned within 30 s with crest partly raised, but quickly lowered it and sang. All of these interactions were entirely silent.

We observed two possible instances of courtship. During the morning and early afternoon of 18 March 1982, Whitney frequently noted the presence of a second Sharpbill foraging in the trees adjacent to the ridgetop male's song perch below the house. This second bird appeared to be ignored on most occasions, but once the male flew to join the other bird in a tree 15 m away. Here the two birds perched very close together on a mossy limb some 12 m above the ground and out of Whitney's direct line of sight. At least one of the birds repeatedly gave a soft, descending chatter of 6–10 syllables that reminded Whitney of a vocalization of *Leptopogon amaurocephalus*. After several repetitions of the chatter, one bird left the tree and flew out of sight, followed 2 s later by the other. Following this, the ridgetop male did not return to his song perch for about 10 min. On 5 April 1982, Stiles twice saw a Sharpbill fly in and land on the ridgetop male's song perch below the house while the male was absent near midday. This individual differed from the ridgetop male in that its iris was orangish and it appeared to have less fluffy crown feathers; it perched silently while looking actively about. On the first occasion, this bird flew off after about 5 min without the male having put in an appearance. On the second occasion, at 1245, the ridgetop male flew directly in and supplanted this bird on the song perch but did not chase it. The second bird flew into a tree some 20 m away and appeared to forage. After singing twice, the male flew into the same tree and perched in dense foliage, apparently close to the other bird but out of sight. Stiles heard several bursts of soft, high-pitched, thin, descending chatters in the next 15–20 s (evidently the same vocalization heard by Whitney); then the birds apparently left the tree heading east or northeast out of Stiles' line of sight. Some 5 min later the ridgetop male flew into a *Clusia* tree behind the house, approaching from the east; after foraging briefly, he flew to his song perch and sang. During the next 1.5 h, no other Sharpbill was seen in his territory. The male's apparent tolerance of these birds near his song perches and the occurrence of a distinct type of vocalization when the two birds were in close contact strongly suggest that these visitors were females and that the interaction observed was courtship. Unfortunately, both of the chattering interactions occurred in foliage too dense for us to see precisely what occurred, although the interaction certainly did not appear to be aggressive.

The nature of these interactions, plus the lack of any long-term association between two Sharpbills, leads us to conclude that the cluster of male territories functions as an exploded lek. Aggressive interactions around song perches between lek males in *Phaethornis superciliosus* and other lek species (Stiles and Wolf 1979 and included references) are strikingly similar to the aggression seen in Sharpbills. The only nonaggressive interactions between Sharpbills seen were the presumed courtships described above, which resemble male-female interactions seen on the exploded leks of some Cotingidae (Snow 1972, 1977). No sign of nesting activity was ever seen in the males' territories, and the fact that the males were apparently continuously present throughout the supposed breeding season argues against any lasting pair bond being formed: in those tyrannine suboscines where a pair bond is formed, the males may not build the nest or incubate but they do help to feed the young (Skutch 1960, 1969). Although the ridgetop male's territory contained several fruiting trees (more in 1981 than in 1982), we saw no overt defense of the trees per se, and our data strongly suggest that much feeding occurred off territory. In Suriname, Davis (in litt.) found clusters of 3–4 singing birds (presumably males) separated by distances of 1–2 km and also concluded that they were exploded leks.

Foraging Behavior

We observed several kinds of foraging behavior by Sharpbills, both for fruits and for arthropod prey. On various occasions we watched a Sharpbill hop deliberately along a moss-laden branch well up in the canopy and probe with the bill into tufts of moss or small epiphytes, sometimes prying small cushions of moss, etc. away from the branch to peer beneath them. The birds also sometimes clung to the sides of branches to peer beneath, like big, slow-moving tanagers (*Tangara*, etc.), again apparently poking and probing into the moss tufts on the branch undersides. Occasionally, Stiles has seen Sharpbills make short, rather clumsy looking sallies, presumably to pluck prey from nearby foliage; such sally-feeding is common in some South American populations of the species (M. P. Fogden pers. comm.) On 3 October 1981 Stiles, T. Moermond, and J. Denslow watched a Sharpbill forage for over 10 min. This bird was deliberately inserting its fine-pointed bill into the tips and edges of tightly rolled young *Clusia* leaves and apparently opening up the leaves by gaping with the bill, often hanging acrobatically in the process. Once it gobbled up something that evidently had been hidden in the rolled leaf. The bird also practiced this technique on rolled dead leaves as we watched. On 20 December 1981 Stiles watched a similar bout of foraging at the rolled young leaves of a strangler fig (*Ficus*) well up in the canopy. The spiders and their egg cases found by Wetmore in Sharpbill stomachs could well have been procured by the poking and prying techniques described here.

Sharpbills were also observed taking fruit on numerous occasions. Sometimes they took small berries (Ericaceae, Loranthaceae, etc.) as described by Slud (1964). The most frequent fruit-foraging we saw, however, was at trees bearing arillate fruits, especially *Hampea appendiculata* (Tiliaceae) and *Clusia oblanceolata* (Guttiferae). The ridgetop male regularly foraged at one *Hampea* and three *Clusia* trees within 100 m of his favorite song perch. In each case, the bird hopped swiftly but heavily in the foliage, grasping the twig and hanging upside-down while inserting the point of its bill into the pods or husks of fruits that were just beginning to dehisce and in which the aril was not yet fully exposed. Prying open the pod, the bird would swallow one or more of the arillate seeds before leaving the fruit. The seeds are evidently regurgitated later, as Stiles found several of the black, shiny *Hampea* seeds under the male's favorite song perch. A number of other birds eagerly eat the arillate seeds of both *Hampea* and *Clusia,* including toucanets, thrushes, tanagers, and flycatchers, such that when we observed them, these trees had very few open fruits with uneaten seeds at any one time. The ability of the Sharpbill to exploit these fruits before they open fully may well give it an advantage in potential competition for them.

It would thus appear that the Sharpbill's sharp bill serves the function of a wedge in prying open rolled leaves and dehiscing fruit and perhaps in prying up tufts of moss, etc. on branches. Strikingly similar pry-and-gape foraging behavior has been well documented in various similarly "sharp-billed" members of the family Icteridae (e.g. Skutch 1954) and in *Vermivora chrysoptera* and *V. peregrina* of the Parulidae (Slud 1964, Morton 1980, Tramer and Kemp 1980). In the forest canopy at La Montura, several other species forage in somewhat similar ways, but we have seen none that duplicates the range of pry-and-gape tactics employed by Sharpbills. The icterids *Cacicus uropygialis* and *Zarhynchus wagleri* regularly pry into moss and epiphytes on branches and (*Cacicus*) rolled dead leaves, especially of palms, but we have not seen them take fruit. The barbet *Eubucco bourcierii* regularly probes rolled dead leaves (cf. Slud 1964), but we have never seen it open rolled young leaves of *Clusia* or *Ficus* or dehiscing fruits. The same applies to the much smaller *Vermivora* warblers, which are probably unable to handle the tough, leathery *Clusia* leaves or take fruits with seeds as large as those of *Hampea* in any case.

CONCLUSIONS REGARDING SHARPBILL RELATIONSHIPS

The Sharpbill's sharp bill and associated foraging behavior would appear to represent a unique specialization in the great cotinga-manakin-flycatcher radiation of the Neotropics. Other aspects of its morphology and biology are perhaps less unusual among its putative relatives in the Cotingidae and Tyrannidae. Sharpbills resemble certain of the larger members of the Cotingidae in their general body proportions and singing behavior and probably in their social system (cf. Snow 1970, 1972, 1977; Wetmore 1972). Their spotted plumage is highly unusual but approached by some other cotingids like *Pipreola* and *Laniisoma.* On the other hand, the concealed reddish crown-patch, modified primary, and flight display somewhat recall certain tyrannids. More information is required to evaluate other known or suspected anatomical peculiarities of Sharpbills properly, such as pterylography, jaw and leg muscles, etc. The nesting habits of Sharpbills remain undescribed, and knowledge of their behavior is still very fragmentary. For the present, it seems safest to continue to recognize the Oxyruncidae as a monotypic family until more data become available.

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(continued on p. 138)

EVIDENCE FOR A POLYPHYLETIC ORIGIN OF THE PICIFORMES

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ABSTRACT.—Despite two recent anatomical studies to the contrary, the order Piciformes appears to be polyphyletic. The structure of the zygodactyl foot in the Galbulae is very distinct from that in the Pici, and no unique shared derived characters of the tarsometatarsus have been demonstrated for these two taxa. The supposedly three-headed origin of M. flexor hallucis longus shared by the Galbulae and Pici is doubtfully homologous between the two groups, leaving only the Type VI deep flexor tendons as defining the order Piciformes. This condition is probably a convergent similarity. Evidence is presented supporting a close relationship between the Galbulae and the suborder Coracii and between the Pici and the Passeriformes. There are fewer character conflicts with this hypothesis than with the hypothesis that the Piciformes are monophyletic. Problems concerning fossil taxa are also addressed. *Received 24 September 1981, accepted 15 May 1982.*

A MONOPHYLETIC origin of the Piciformes appears to have gained support from the simultaneous appearance of two cladistic, anatomical papers (Swierczewski and Raikow 1981, Simpson and Cracraft 1981) that concur in the traditional concept of the order—a concept that has prevailed at least since the time of Gadow (1893). I depart from this view in considering each of the two major subdivisions of the Piciformes, the Galbulae (Bucconidae, Galbulidae) and the Pici (Capitonidae, Ramphastidae, Indicatoridae, Picidae), to be more closely related to another group than to each other. My purpose here is (1) to show that the evidence for monophyly is weak, uncorroborated, and has in part been misrepresented by Simpson and Cracraft (1981), and (2) to make preliminary suggestions as to the probable closest relatives of the Galbulae and the Pici.

THE WEAKNESS OF THE EVIDENCE FOR PICIFORM MONOPHYLY

Zygodactyly.—Obligate zygodactyly, the condition in which the fourth toe is permanently reversed and has an enlarged accessory articulating process (the "sehnenhalter"), occurs in cuckoos (Cuculidae, Cuculiformes), parrots (Psittacidae, Psittaciformes), and in the Piciformes. This is obviously a derived condition in birds that could be used to define these taxa as a monophyletic group in a cladistic sense, unless it were shown that each of these zygodactyl taxa shares derived characters with outside groups in a manner indicating that the zygodactyl condition in cuckoos, parrots, and Piciformes had arisen independently, through convergence.

Although I certainly do not advocate a monophyletic origin of zygodactyl birds, the arguments that Simpson and Cracraft (1981) and Swierczewski and Raikow (1981) present against such a hypothesis do not meet the requirements of their cladistic methodology. Simpson and Cracraft (1981: 484) conclude only that "the relationships of cuckoos and parrots remain among the most enigmatic within ornithology . . . ," although "there is a general acceptance among avian systematists . . . that piciforms are most closely related to coraciiforms or to passeriforms and that cuckoos and parrots are not." They concede that "this hypothesis has yet to be tested cladistically . . . ." Swierczewski and Raikow (1981: 469) state that: "The muscular component of the foot mechanism is quite different in [the Cuculidae, Psittacidae, and Piciformes] . . . which supports the contention (Bock and Miller 1959: 30) that those groups became zygodactyl independently." Both sets of authors have thus tacitly accepted differences between taxa as evidence of nonrelationship, a procedure of which Cracraft has been outspokenly critical (see Olson 1982).

The most complete and original work on the nature of the zygodactyl foot is that of Steinbacher (1935), whose results have seldom been accurately represented (a notable exception being Sibley and Ahlquist 1972). Steinbacher

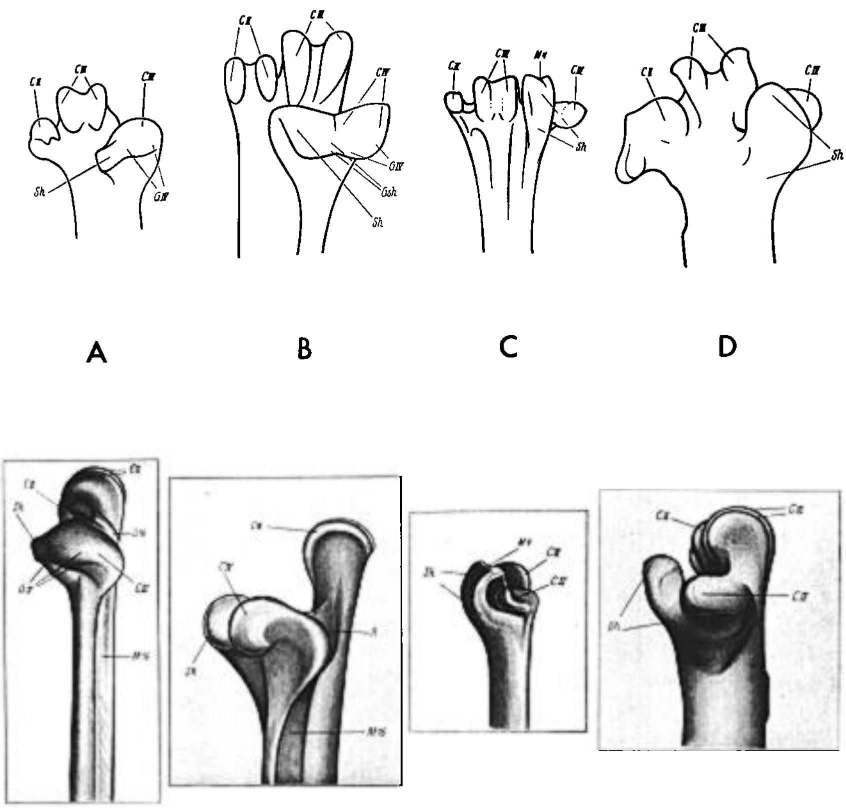

Fig. 1. Posterior (top row) and lateral (bottom row) views of the distal end of the tarsometatarsus in the four groups of birds with obligate zygodactyly (illustrations from Steinbacher 1935). A, cuckoo, *Centropus ateralbus* (Cuculidae, Cuculiformes); B, jacamar, *Galbula ruficauda* (Galbulidae, Galbulae, "Piciformes"); C, toucan, *Ramphastos toco* (Ramphastidae, Pici, Piciformes); D, parrot, *Amazona ochrocephala* (Psittacidae, Psittaciformes). Abbreviations: Sh = sehnenhalter, C II = trochlea for digit II, C III = trochlea for digit III, C IV = trochlea for digit IV, G IV = articulating surface for digit IV, Gsh = articulating surface of sehnenhalter, M 16 = depression for origin of M. extensor brevis digiti IV, R = groove for tendon of M. extensor brevis digiti IV, M 4 = depression for tendon of M. flexor perforatus digiti IV. It can be seen that the form of zygodactyly in the Galbulae is completely different from that in the Pici, and the two can in no way be regarded as homologous. The best interpretation of the evidence from the tarsometatarsus is that zygodactyly evolved independently in all four of these groups.

showed that there were *four* distinct types of morphology of the tarsometatarsus in birds with obligate zygodactyly, with that in the Galbulae being as different from that in the Pici as either of these two is from parrots or cuckoos (Fig. 1). In each of these four groups there is a sehnenhalter. Steinbacher (1935: 234) even identified a sehnenhalter in owls (Strigiformes), which are facultatively zygodactyl. Thus, the statement by Simpson and Cracraft (1981: 485) that "zygodactyly and the presence of a sehnenhalter can be interpreted as derived characters defining the piciforms as monophyletic" is disingenuous. In citing Steinbacher (1935) as providing evidence "that osteological . . . characteristics of zygodactyly are distinct for the piciforms and different from cuckoos and parrots," Simpson and Cracraft (1981: 484) have clearly misrepresented the facts and Steinbacher's interpretation of them.

Nowhere do Simpson and Cracraft, nor any other authors (e.g. Bock and Miller 1959), show that there are derived characters of the tarsometatarsus that will distinguish the Galbulae and Pici from parrots and cuckoos and that will establish the Piciformes as a monophyletic group. In fact, the apparently less modified trochlea IV and sehnenhalter in the Galbulae are actually more similar to the condition in cuckoos, whereas the larger, more discrete, and distally projecting sehnenhalter in the Pici is more like that in parrots (Fig. 1). There simply is no evidence in the structure of the tarsometatarsus that will demonstrate a close relationship between the Galbulae and the Pici.

Swierczewski and Raikow (1981) present six myological characters to define their Clade B (= Galbulae) and six additional myological characters to define their Clade G (= Pici). Thus, these two taxa differ from each other in at least 12 myological characters of the hind limb, as well as having a completely different structure of the tarsometatarsus associated with their respective forms of zygodactyly. May we not, then, apply the same statement that Swierczewski and Raikow used against monophyly of all zygodactyl birds to argue against monophyly of the Piciformes, namely that "the muscular component of the foot system is quite different in those groups," a difference supporting the contention that they "became zygodactyl independently" (Swierczewski and Raikow 1981: 469)?

Origin of M. flexor hallucis longus.—Swierczewski and Raikow state that M. flexor hallucis longus has three heads in the Piciformes, which they interpret as a derived condition that supports monophyly. Simpson and Cracraft (1981: 483) imply this condition to be unique to the Piciformes by stating that "the muscle arises by one or two heads in other birds," whereas Swierczewski and Raikow discuss the fact that M. flexor hallucis longus also has three heads in most passerines. Because the lateral head has a different relationship to the tendon of M. iliofibularis in Passeriformes, Swierczewski and Raikow (1981: 473) consider that the "condition in the two orders is therefore probably not homologous." At this point I would also question whether the condition in the Galbulae and Pici has been established as being homologous.

Before I was able to consult Swierczewski's (1977) unpublished dissertation for details, I dissected one specimen each of the barbet *Trachyphonus darnaudii* (Capitonidae: Pici) and the puffbird *Hypnelus bicinctus* (Bucconidae: Galbulae) in order to assess the configuration of M. flexor hallucis in each. In the normal avian condition, this muscle originates in the popliteal fossa of the femur. In the specimen of *Hypnelus* that I examined, the origin was expanded so that fibers also originated from the proximal end of the fibula and from the median raphe of the adjacent M. flexor perforatus digiti III. [Incidentally, Fig. 6d in Simpson and Cracraft (1981) is mislabelled—"Fpp3" should read "Fp3."] In *Trachyphonus* the fibers originating on the fibula, and those originating on the raphe of M. flexor perforatus digiti III, are slightly separated from the main belly of the muscle that originates in the popliteal fossa, thus making the muscle three-headed. Clearly, M. flexor hallucis longus, in contributing to the flexion of two toes in addition to the hallux, has become strengthened by expanding the area of its origin to the two nearest available structures. This is directly correlated with the Type VI arrangement of the flexor tendons and is part of the same character complex.

I could not detect any separate heads of origin in the bucconid *Hypnelus*, however. Indeed, Swierczewski (1977: 57) states that in the Galbulidae and Bucconidae the heads are "somewhat difficult to separate from each other." He also notes that the "common belly extends only about two-thirds the length of the tibiotarsus" in the Galbulae, versus almost the entire length of the tibiotarsus in the Pici. Thus, it seems far from certain that the nature of the origin of this muscle is homologous between the Galbulae and the Pici or even that it can really be said to have three heads in the Galbulae.

Type VI flexor tendons.—Gadow (1893) defined the Piciformes by their possession of the Type VI configuration of the deep flexor tendons, whereby M. flexor hallucis longus, which ordinarily has a direct tendinous connection only with the hallux (digit I), flexes digits II and IV as well, and M. flexor digitorum longus flexes only digit III. This condition must have arisen when digit IV was reversed and began to function as a second hallux (zygodactyly). That parrots and cuckoos are zygodactyl but do not have the Type VI flexor tendons is evidence that different evolutionary pathways can produce similar functional results.

The Type VI tendon arrangement was used originally to define the Piciformes, and it is still the only character that can be cited to unify the order. Given that the condition of origin of M. flexor hallucis longus is part of the same complex and is doubtfully homologous in the Galbulae and Pici anyway, then it may fairly be said that the new studies of osteology and

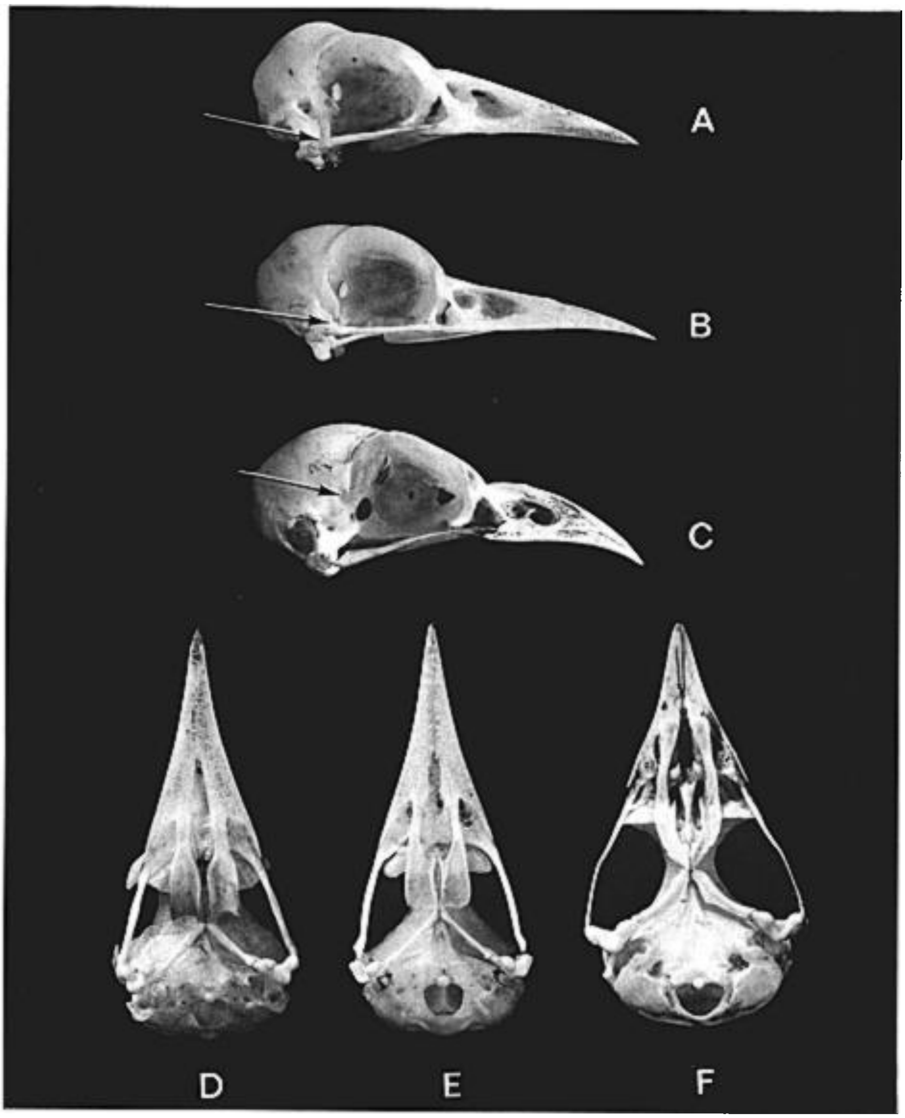

Fig. 2. Lateral and ventral views of skulls of a roller, *Coracias benghalensis* (A,D); a puffbird, *Malacoptila panamensis* (B,E); and a barbet, *Trachyphonus purpuratus* (C,F). Note the great overall similarity between the roller (Coraciidae) and the puffbird (Bucconidae), whereas neither closely resembles the barbet (Capitonidae). The arrows indicate the ventral extent of the postorbital process, which is greatly developed in the Coracii and Galbulae. Not to scale.

myology of the Piciformes have failed to reveal a single new character that independently corroborates the hypothesis of monophyly.

If we consider that the Piciformes are *not* monophyletic, then the Type VI condition of the flexor tendons must have arisen more than once. This is not at all an unreasonable hypothesis. Convergence in myological characters occurs with great frequency, as Swierczewski and Raikow (1981) amply demonstrate. Of the 43 myological characters presented in their Table 1, 40% evolved more than once *just within the Piciformes*. With the probability of convergence being so high, it is clearly impractical to justify an entire order of birds with a single myological character. In another situation, Berman and Raikow (1982: 55) found that only colies (Coliidae) and parrots have a branch of the M. extensor digitorum longus tendon extending to the hallux; yet, they considered that "this character alone cannot demonstrate a common ancestry for the Coliiformes and Psittaciformes . . . ." Why, then, should a single tendinal character be accepted as demonstrating the common ancestry of the Piciformes?

THE RELATIONSHIPS OF THE GALBULAE AND THE PICI

Here, I will briefly outline my reasons for believing the Galbulae to be closely related to the rollers, or Coracii of Maurer and Raikow (1981), which includes the Coraciidae, Brachypteraciidae, and Leptosomidae. The Pici, on the other hand, I believe are more closely related to the Passeriformes. These observations are preliminary; a more complete assessment of the interrelationships of all the higher orders of land birds requires more evidence than is now available. For example, it is difficult to make myological comparisons of the Piciformes and Coraciiformes from the existing literature because Swierczewski and Raikow (1981) and Maurer and Raikow (1981) have presented only the evidence that supports their classifications, while omitting the descriptive observations of actual dissections. Even with access to the unpublished dissertations of Swierczewski (1977) and Maurer (1977), cross comparisons are difficult, because a character that was deemed important in one group was often not considered significant in the other, so that certain descriptions may be inadequate for comparison, necessitating the re-examination of specimens.

Sibley and Ahlquist (1972) have previously suggested a relationship between the Galbulae and the Coraciiformes, but they particularly singled out the kingfishers (Alcedinidae) as possible affines. The kingfishers, however, belong to the alcedinine group of Coraciiformes that is characterized by a derived morphology of the stapes (Feduccia 1975) and several derived myological characters (Maurer and Raikow 1981) that do not occur in the Galbulae. A lack of relationship between the Galbulae and the Alcedinidae does not, however, preclude a relationship between the Galbulae and some other section of the Coraciiformes.

The skull and mandible in the Galbulae, particularly in the less-specialized family Bucconidae, show a remarkable similarity to those of *Coracias* (Coraciidae) in almost every aspect (Fig. 2)—bill shape, truncate palatines, straight and narrow pterygoids, heavily ossified nasal septum, shape and position of the temporal fossae, the inflated ectethmoid plate, and the greatly exaggerated and ventrally produced post-orbital process. In all of these characters the Bucconidae are consistently different from the Pici.

The major differences between the skulls of the Bucconidae and *Coracias* are in the reduced lacrimal and the dorsal expansion of the palatines onto the parasphenoid rostrum in the Bucconidae. These differences are more like those observed between genera within a family than between different orders. They are less profound than the differences observed between the four families of Pici, for example. In many respects, the skull of *Coracias* differs less from that of the bucconid *Malacoptila* than it does from *Eurystomus*, the only other modern genus in the Coraciidae.

In the Galbulae, and in all of the Coracii, the postorbital process is greatly enlarged and extends straight ventrally as far as the jugal bar (Fig. 2). From this there is a very strong, short, post-orbital ligament that attaches to a process on the medial surface of the mandible just anterior to the articulation (Fig. 3). The M. adductor mandibulae complex is correspondingly narrowed, enabling it to pass through the relatively small foramen formed by the enlarged postorbital process (Fig. 3). On the other hand, the postorbital process is quite small in the Pici, most Passeriformes, the Trogonidae, and in the remainder of the Coraciiformes except the Bucerotidae and some of the Momotidae. In the last two instances, the postorbital process is well developed but does not extend nearly as far ventrally as it does in the Coracii and the Galbulae. In the one example of barbet (*Trachyphonus darnaudii*) that I dissected, the postorbital ligament was very weak and was scarcely differentiated from the overlying fasciae.

In the elements of the postcranial skeleton of the Galbulae, there is greater similarity to the Coracii than to the Pici. The coracoid in the Galbulae is almost identical to that in the roller group (Fig. 4) and is very different from that found in the Pici. The humeri and carpometacarpi in the Galbulae are also more similar to those in the rollers than to the Pici (see below).

Those who have experience identifying

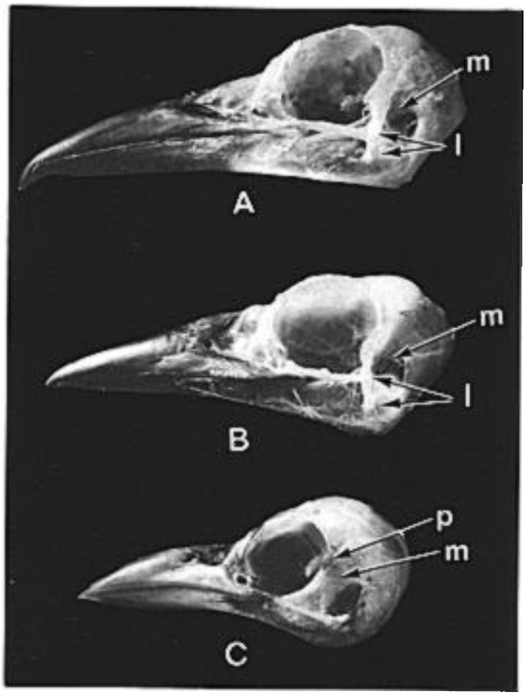

Fig. 3. Dissected heads of a roller, *Coracias garrulus* (A); a puffbird, *Notharchus pectoralis* (B); and a barbet, *Trachyphonus darnaudii* (C). Note the marked similarity between the roller and the puffbird in the very strong ligament (l) from the enlarged postorbital process to the mandible and in the narrowed adductor mandibulae complex (m), whereas in the barbet the postorbital process (p) is very small, the ligament is vestigial, and the adductor mandibulae complex is of more normal development. Not to scale.

isolated bird bones are aware of the skeletal similarities between the Pici and the Passeriformes; a possible relationship between these two groups has long been recognized (see Sibley and Ahlquist 1972). Lowe (1946) considered the Pici to be but a suborder of the Passeriformes and did not include or even mention the Galbulae.

The coracoid in the Pici and Passeriformes is very slender and elongate, with the sternal end and head narrow, the sterno-coracoidal process reduced, and the procoracoid process usually vestigial or even absent (Fig. 4). This contrasts with the condition in the Galbulae and most Coraciiformes, in which the coracoid is comparatively short, the head and sternal end expanded, and the sterno-coracoidal and procoracoid processes well developed. The carpometacarpus in the Pici differs from that in the Galbulae and Coraciiformes in having a broad and very well-developed intermetacarpal tubercle, a condition shared only with the Passeriformes among the higher land birds. The humerus in the Pici differs from that in the Galbulae and Coraciiformes and resembles that in the Passeriformes in having the shaft short and stout, the proximal end broader, and the deltoid crest squared, rather than triangular or rounded.

Whereas we have seen that no characters independent of the deep flexor tendons could be found to corroborate piciform monophyly, most other characters, whatever their "polarity" may be, are concordant when the Galbulae are allied with the Coracii and the Pici are allied with the Passeriformes. Thus, the oil gland is covered with down and lacks a tufted orifice in the Galbulae and Coracii but is nude, with a tufted orifice, in the Pici and Passeriformes (Gadow 1896). The caeca are well developed in the Gabulae and Coracii but absent or rudimentary in the Pici and Passeriformes (Gadow 1896; pers. obs. for Galbulae). The structure of the down in the Galbulae is like that of the Coracii, whereas that of the Pici is similar to that of the Passeriformes (Chandler 1916). Of the six derived myological characters that Swierczewski and Raikow use to define the Pici, four (characters 1, 33, 39, and 41) are found in most, some, or all passerines. Mm. popliteus, adductor digiti II, and extensor brevis digiti IV are absent in the Pici (characters 33, 39, and 41) and in Passeriformes, whereas each of these muscles is present in both the Galbulae and the Coracii. If my interpretation of Maurer's (1977) descriptions is correct, four characters (15, 29, 31, and 32) of the six that Swierczewski and Raikow (1981) use to define the Galbulae as monophyletic also occur in the Coracii, whereas only two (14 and 42) appear to be unique (autapomorphous). When all of the data can be analyzed, I am confident that there will be far fewer character conflicts when the Piciformes are split apart, as I have proposed here, than when they are maintained as monophyletic.

COMMENTS ON FOSSIL TAXA

Simpson and Cracraft's (1981: 491) discussions of the Primobucconidae and Zygodactylidae are misleading. Their statement that the

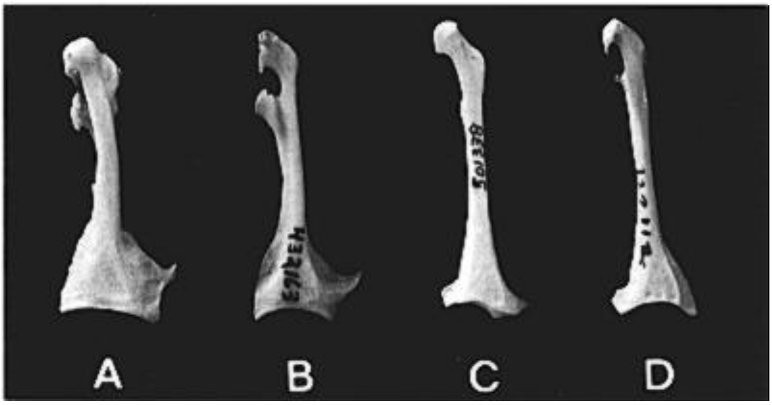

Fig. 4. Ventral view of coracoids to show the similarities between the ground roller *Brachypteracias leptosomus* (A), and a puffbird, *Malacoptila panamensis* (B). These differ greatly from the coracoid in the Pici (C, the woodpecker, *Colaptes auratus*), which is more like that in passerines (D, a rhinocryptid, *Pteroptochos megapodius*). Not to scale.

Primobucconidae have not been shown to be a monophyletic group is irrelevant. Such a statement could truthfully be made about the vast majority of groups of birds or other organisms. Simpson and Cracraft present no information to suggest that the primobucconids are *not* monophyletic. Their contention that "the bucconids and galbulids are fully zygodactyl," but that the "Eocene genera [of primobucconids] are not," hinges entirely on the definition of "fully zygodactyl," which they do not provide. Two specimens of primobucconids (the holotype of *Neanis kistneri,* Feduccia 1973; and the holotype of *Primobucco olsoni,* Feduccia and Martin 1976) are preserved with the outer toe completely reversed, in the zygodactyl manner. Perhaps by "fully zygodactyl" Simpson and Cracraft mean that the primobucconids do not have the fourth trochlea and sehnenhalter as modified as in other zygodactyl birds, but the primobucconids were certainly functionally zygodactyl. [Note also that Simpson and Cracraft (1981: 491) misquote Feduccia and Martin (1976)—the description of the primobucconid tarsometatarsus should read "a distinct groove *separating* the posterior portion of the trochlea" not "supporting" it.]

Simpson and Cracraft contend that the more primitive tarsal morphology of the primobucconids argues against their being placed within the Galbulae, but this follows only if one defines the Galbulae solely by the possession of a completely modified fourth trochlea. At some point, the Galbulae obviously had ancestors that were not zygodactyl, and forms transitional between those ancestors and the fully zygodactyl modern Galbulae must have existed. The Galbulae would have to be included at some taxonomic level with birds that did not have the fourth trochlea as modified as do the modern members of the suborder. Because Simpson and Cracraft present no evidence to show that the primobucconids are more closely related to some other group, there is no reason not to follow Brodkorb (1970) and Feduccia and Martin (1976) in considering the Primobucconidae to be primitive members of the Galbulae that share more similarities with the Bucconidae than with any other extant family of birds.

Simpson and Cracraft (1981: 492) tentatively suggest "placing the Zygodactylidae as a basal member of the Pici," but they present no evidence for this either. Ballmann (1969a, b) deliberately did not put *Zygodactylus* in any existing order, because he considered that its affinities could not be determined from the tarsometatarsus and tibiotarsus, the only elements yet known. For descriptive purposes he made comparisons not only with the Piciformes but also with the Psittaciformes. Ballmann (pers. comm.) has emphasized verbally to me his belief that *Zygodactylus* is not piciform. If *Zygodactylus* tells us anything at this point, it is probably that the specialized zygodactyl condition of the tarsometatarsus, in which the fourth trochlea becomes enlarged and bears a sehnenhalter, has evolved yet another time.

CONCLUSION

As I have indicated elsewhere (Olson 1981), the higher level systematics of birds has a very poor foundation. The questions of whether or not currently recognized orders are monophyletic and what the interrelationships of these orders may be are still largely unanswered. Although the studies of Swierczewski and Raikow (1981) and Maurer and Raikow (1981) are useful in documenting the monophyly of some of the subunits of Coraciiformes and Piciformes, at the level of ordinal and interordinal systematics they are less successful. Despite these workers' accumulation of much new data, they could recognize the orders Piciformes and Coraciiformes as monophyletic only by the configuration of the deep flexor tendons—the same character that had been used to define these orders nine decades ago. Their studies were designed only so as to test hypotheses that had previously been formulated, whereas they seem to lack the means to generate alternative hypotheses. Herewith, I have supplied one for the Piciformes, and there is every reason to expect alternative hypotheses of relationships for the Coraciiformes and for other orders based on single characters or that are otherwise poorly defined.

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MONOPHYLY OF THE PICIFORMES: A REPLY TO OLSON

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ABSTRACT.—Olson (1983) questioned the hypothesis that the order Piciformes is monophyletic and suggested instead that each piciform suborder is allied with a nonpiciform group. His attempt to discredit the synapomorphies joining the Galbulae and Pici is refuted by corrections of his interpretations of previous work. The Piciformes share a complex derived hindlimb morphology involving zygodactyly, a tripartite flexor hallucis longus, and Type VI flexor tendons. Olson's argument for polyphyly combines inadequate data with the inappropriate technique of equating general overall similarity with affinity. His hypothesis is therefore rejected. Problems concerning fossil taxa are also discussed. Based on current information, we believe that a monophyletic origin of the Piciformes remains the hypothesis of choice. *Received 18 August 1982, accepted 18 October 1982.*

SWIERCZEWSKI and Raikow (1981) and Simpson and Cracraft (1981) studied the phylogenetic relationships of the Piciformes. Both concluded that the order is monophyletic and that it contains two monophyletic suborders, the Galbulae (Bucconidae and Galbulidae) and Pici (Capitonidae, Ramphastidae, Indicatoridae, and Picidae). Olson (1983) criticizes the hypothesis of monophyly. First, he questions the arguments supporting this view. He then presents an alternative hypothesis that the Galbulae are most closely related to the Coracii and the Pici to the Passeriformes. Finally, he criticizes Simpson and Cracraft's discussion of certain fossil birds. After carefully examining Olson's critique, we believe that monophyly remains the more strongly supported hypothesis. The possible value of these discussions goes beyond the question of a single branching point in a phylogeny, as it provides an opportunity to compare and contrast two profoundly different approaches to systematic analysis.

PICIFORM MONOPHYLY

Zygodactyly.—Olson suggests that zygodactyly arose independently in the Pici and Galbulae because Steinbacher (1935) found differences in their tarsometatarsi. He does not consider the possibility that the differences arose after the two groups diverged from a zygodactylous common ancestor. Olson considers that the tarsometatarsus of the Galbulae is more primitive than that of the Pici, which is more "specialized," and therefore that monophyly requires the condition in the Pici to have evolved from that in the Galbulae. Here, he confuses sister-group relationship with ancestor-descendent relationship. We did not propose that the Pici evolved from the Galbulae (higher taxa cannot be ancestors). Olson asks ". . . why would such a transformation take place? Once a group of birds has become permanently zygodactyl, is it possible to become *more* zygodactyl?" This question manifests a confusion. One group is not "more zygodactyl" than the other; both are described by this term. It may be expected, however, that differences will accumulate in separately evolving lineages after they have split; it is this process of evolutionary divergence or character transformation that gives rise to the hierarchical structure of organic diversity. We suggest that the zygodactyl conditions of the Galbulae and Pici are homologous because other characters (see below) corroborate the unity of the Piciformes.

M. flexor hallucis longus.—Swierczewski and Raikow (1981) reported that the flexor hallucis longus muscle (FHL) shows a derived condition in its origin by a certain pattern of three heads. In most birds there are one or sometimes two femoral heads, but the Piciformes have as well an extensive origin from the fibula. Olson dissected one capitonid (*Trachyphonus*; Pici) and one bucconid (*Hypnelus*; Gal-

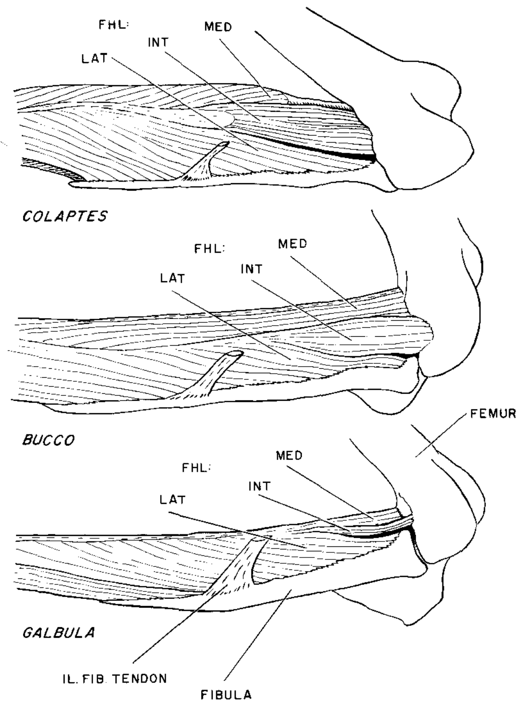

Fig. 1. Lateral views of the region of the knee and upper crus in three species of piciform birds to show the mode of origin of M. flexor hallucis longus (FHL). In all Piciformes the muscle arises by three separate heads, medial (MED), intermediate (INT), and lateral (LAT), all of which lie medial to the tendon of M. iliofibularis (IL. FIB.). The representative forms illustrated are *Colaptes auratus* (Picidae; Pici), *Bucco tamiata* (Bucconidae; Galbulae), and *Galbula dea* (Galbulidae; Galbulae). The drawings were made with a camera lucida and dissecting microscope and are not to scale.

bulae). In *Trachyphonus* he confirmed the report of Swierczewski and Raikow (1981), but in *Hypnelus* he did not. Olson quotes Swierczewski (1977: 57) as saying that in the Galbulae the heads are "somewhat difficult to separate from each other." Swierczewski's *full* statement, however, conveys a different meaning: "In the Galbulidae and Bucconidae, the medial head arises semitendinous from the intercondyloid region of the femur, and the intermediate head arises fleshy from the proximocaudal surface of the external femoral condyle; the heads being somewhat difficult to separate from each other." This statement refers to only two of the three heads; it does not refer to the fibular head, which is the significant structure. Olson dissected one specimen each of two species. In contrast, Swierczewski dissected between one and four specimens each of 45 species, and concluded unequivocally (1977: 58) that "Three heads of origin were found in all species studied herein."

Nevertheless, one of us (R.J.R.) has, in response to Olson's comments, dissected the limb of *Colaptes auratus* (Picidae), *Bucco tamiata* (Bucconidae), and *Galbula dea* (Galbulidae). Like Olson, Raikow confirmed in *Colaptes* the three heads previously described (Fig. 1). In *Hypnelus*, Olson ". . . could not detect any separate heads of origin . . ." and questioned whether ". . . the nature of the origin of this muscle is homologous between the Galbulae and the Pici or even that it can really be said to have three heads in the Galbulae." The dissection of *Galbula* and *Bucco* has fully confirmed our previous report that the three heads, including the large fibular head, are present in the pattern described (Fig. 1). This corroborates the hypothesis of piciform monophyly and refutes Olson's claim that the condition is not found in both piciform suborders.

Type VI flexor tendons.—Did this condition arise once in the Piciformes or separately in the Galbulae and Pici? Olson states that it is "probably a convergent similarity," but offers no evidence. He suggests that the Galbulae would be difficult to identify with their feet cut off, but fortunately all of our specimens possessed feet. (Actually, the relevant structures are legs, not feet, as the FHL belly lies in the crus.) Olson feels that such characters do not justify *ordinal* rank, but we do not agree that taxonomic rank is related to the corporeal location of the relevant characters. Here, Olson confuses phylogeny with taxonomy; the question at issue is whether the group is monophyletic, not what rank it should have in a classification. Perhaps the FHL should rank the group at the generic level, because its origin lies at the knee joint (*Junctura genus*).

Analysis of Olson's Hypothesis

Inadequate data.—Olson compares characters in only some of the relevant groups, so that comprehensive comparisons cannot be made. For example, he notes that "in plumage pattern, the ground roller *Brachypteracias leptosomus* is quite similar to certain of the Bucconidae such as *Malacoptila.*" But what are the patterns in the other Coracii, the other Bucconidae, and the Galbulidae? Why are they not discussed? Convergence in plumage patterns is common, which is why comprehensive comparisons are needed to distinguish between synapomorphies and spurious resemblances.

Again, in discussing the skull Olson argues for similarities between the Galbulae and Coracii, but restricts his comparison almost entirely to the Bucconidae and *Coracias* when listing several features. "In all of these characters," he notes, "the Bucconidae are consistently different from the Pici." But what about the Galbulidae and other Coracii?

This pattern of selective, almost casual choice of data characterizes Olson's entire presentation. It is also difficult to assess his data, because they are presented in a narrative form within the text but are not tabulated in a way that would allow one to determine the state of each character in all the relevant taxa. A tabulation of this sort would have revealed that broad conclusions are often based on little data; e.g. Olson dissected only one barbet to determine the form of the postorbital ligament in the large and diverse suborder Pici.

Incorrect determination of polarity.—Although generally eschewing cladistic methods, Olson does make one attempt to show the derived nature of a condition, the complex of the postorbital process, postorbital ligament, and adductor mandibulae. He considers this derived because it ". . . does not occur in *Archaeopteryx*, in presumably primitive land birds such as *Opisthocomus* and the Cuculiformes, or elsewhere in the higher groups of land birds." Several problems invalidate this conclusion. First, there is no reason to assume that a character is primitive because it occurs in "primitive" taxa. All taxa, including fossil forms, are mosaics of primitive and derived characters. Second, while we concede the general primitiveness of *Archaeopteryx*, we question the extent to which the ligament and muscle can be reconstructed in it. Furthermore, on what basis are the Cuculiformes and *Opisthocomus* "presumably primitive"? What are "higher groups" of land birds? Why is the comparison limited to the nonmonophyletic nontaxon of *land* birds? Olson's analysis fails to show that the condition is derived, or even that it is generally characteristic of the groups involved.

Use of phenetic similarity.—The basic problem with Olson's study is that he tries to determine phylogenetic relationships by phenetic similarity. He claims that we accept the idea that ". . . differences between taxa [are] evidence of nonrelationship . . . ," but this is incorrect. We mean only that the absence of similarities fails to corroborate a hypothesis of monophyly, not that the presence of differences refutes such a hypothesis. "Nonrelationship" has no intrinsic meaning; we are searching for patterns of common ancestry identified by synapomorphy.

The problem with phenetic comparisons is that characters are not analyzed so as to identify the level within the phylogenetic hierarchy at which they define taxa. To illustrate this point, we will consider one example from a recent study of the relationships of *Pedionomus torquatus*. This species is placed in the monotypic family Pedionomidae, and the problem is to find its closest relatives. Olson and Steadman (1981) rejected the previous hypotheses that it is related to the Turnicidae (Gruiformes) or the Galliformes and concluded that it belongs in the Charadriiformes. Olson and Steadman (1981: 3) note that a hallux is present in *Pedionomus* and most Charadriiformes but is absent in the Turnicidae. They consider (p. 21) that this supports the removal of *Pedionomus* "from the vicinity of the Turnicidae and its placement in the Charadriiformes." Actually, it does nothing of the kind. The hallux evolved in vertebrates as part of the transformation of the pelvic fin into a limb. As such, it is a derived character at the level of the Tetrapoda. Inasmuch as birds form a tetrapod subgroup, the presence of a hallux is a primitive state and reveals nothing about the relationships of any avian species to any other. It tells us *one thing only* about *Pedionomus*, namely that it is a member of the Tetrapoda. It definitely refutes any hypothesis that *Pedionomus* is a fish, but that is all it does.

This example illustrates the principle that character comparisons convey maximum information about phylogenetic relationships only when one determines the specific points at which they are relevant within the nested system of clades forming a phylogeny. Simplistic phenetic comparisons fail to provide this information. Olson's assessments of "similarity" cannot be interpreted, because we do not know which of them represent shared primitive characters and which derived for any group of species. The necessity for such analysis may be emphasized by pointing out the distinction between similarity and phylogenetic relationship, namely that they do not necessarily coincide. When an evolving lineage splits, one daughter lineage may evolve faster than the other, so that a form may be less similar to a genealogically closer relative than to a more distant one. Lungfishes are more similar to goldfishes than they are to goldfinches, but they are more closely related to goldfinches than to goldfishes. Crocodiles are more similar to turtles than to turtle doves, but they are more closely related to turtle doves than to turtles. Such statements are based on the idea that relationship is defined by recency of common ancestry and are correct within the context of specific phylogenetic hypotheses, in this case those of Wiley (1979). Genealogical relationships are postulated by the recognition of patterns of monophyly, which are defined by synapomorphy. For extended discussions of this principle, see Eldredge and Cracraft (1980), Wiley (1981), and Raikow (1982).

DISCUSSION OF FOSSIL TAXA

The section of Olson's critique "Comments on Fossil Taxa" adds nothing new about the systematics of the taxa placed in the Primobucconidae and Zygodactylidae but does illustrate the limitations of his systematic methodology. Simpson and Cracraft (1981) pointed out that no evidence exists to support the monophyly of the Primobucconidae; Olson in contrast, believes that this observation is "irrelevant." But inasmuch as the "primobucconids" have played a pivotal role in the speculations of Olson and his colleagues about the history of the North American bird fauna, it does not seem "irrelevant" to us to ask whether the Primobucconidae have any objective reality as a natural group. Indeed, if the primobucconids are not monophyletic, then Olson and his colleagues are constructing evolutionary scenarios based upon an imaginary taxon. As a consequence, one might expect that Olson would want to demonstrate that monophyly. His critique, however, is a weak attempt to defend the conclusions of Feduccia and Martin (1976) and lacks any relevant empirical evidence.

Olson's attempt to shift the burden of proof onto Simpson and Cracraft is altogether spurious. We suggest that the burden of proof lies with workers who erect a taxon without positive evidence for its existence as a geneaological unit. Present morphological evidence suggests that the Primobucconidae are a grade, not a clade. If so, then the family has no ontological status, and Olson should instead be defending the usefulness of discussing the evolution of a fictitious taxon.

Simpson and Cracraft (1981: 491) were very specific in their criticism; none of the taxa of the Primobucconidae is known to have an enlarged sehnenhalter. For that reason, they concluded that there is no justification for saying that the primobucconids are piciforms as currently accepted, let alone closely related to the Bucconidae. That conclusion, if true, also falsifies Olson's unsupported speculations about the independent origin of zygodactyly in the Galbulae. From our standpoint, the latter group was already zygodactylous when it arose, because the origin of zygodactyly took place at a higher hierarchical level. This is why Simpson and Cracraft (1981: 491) suggested that one or more taxa currently included in the Primobucconidae might be the sister group of the Piciformes.

Olson's comments about the Zygodactylidae contain further inaccuracies. Simpson and Cracraft (1981: 492) *did* provide evidence for including this fossil taxon in the Pici, namely an advanced form of the sehnenhalter, but they also stressed the very tentative nature of this placement. Furthermore, Simpson and Cracraft did not voice any major disagreement with Ballman's (1969a, b) interpretations, as implied by Olson. Their disagreement was with the placement of the Zygodactylidae in the Galbulae (Brodkorb 1971). Simpson and Cracraft specifically stated that Ballman may be correct in believing that *Zygodactylus* is not a piciform.

CONCLUSIONS

Rather than reply to every individual point raised by Olson, we have instead addressed the basic differences in systematic philosophy that exemplify current controversy in biology. Olson's attempt to question the synapomorphies linking the Galbulae and Pici stands refuted; the Piciformes are characterized by a complex derived morphology of the hind limb involving zygodactyly, tripartite flexor hallucis longus, and Type VI tendons. Olson supports his hypothesis with a potpourri of casual phenetic similarities analyzed by inappropriate methods, and his argument is little more than an opinion. On the basis of present understanding, we conclude that piciform monophyly remains the preferred hypothesis.

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WHY DO BROWN-HEADED COWBIRDS PERFORM THE HEAD-DOWN DISPLAY?

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ABSTRACT.—Four hypotheses for the function of the head-down display performed by Brown-headed Cowbirds were tested with observational data from free-ranging and captive cowbirds. Free-ranging cowbirds performed 284 interspecific and four intraspecific displays during 59.2 daylight hours while roosting in mixed-species flocks adjacent to feeding areas. The most common recipients of displays, female Red-winged Blackbirds and House Sparrows, preened cowbirds during 25 displays. Cowbirds that had just been preened displayed more often than those that had not recently been preened. Captive cowbirds displayed intraspecifically 475 times during 13.3 h, and dominant captive birds displayed more often than their subordinates. The following hypothesis was proposed to explain the display's function: the head-down display of Brown-headed Cowbirds is an appeasing agonistic behavior, the displayor is most often dominant to the recipient, and subsequent displaying is stimulated by interspecific preening. The display may function in: (a) obtaining food, (b) minimizing roosting energetics, and/or (c) establishing flock order. *Received 26 November 1979, resubmitted 5 January 1982, accepted 30 August 1982.*

BROWN-HEADED COWBIRDS (*Molothrus ater*) perform an unusual head-down display (Darley 1968) during which they direct the backs of their heads and necks toward other birds (Selander and La Rue 1961). The head-down display, also called the preening invitation display (Selander and La Rue 1961), is performed both intra- and interspecifically (Selander and La Rue 1961; Stevenson 1969; Rothstein 1977, 1980; Scott 1977). Interspecific displays may include, in addition to the above posture, the preening of the displaying cowbird's feathers by the display recipient (Selander and La Rue 1961, Scott 1977). Several other species of cowbirds perform a display similar, but not identical, to that of the Brown-headed Cowbird (Selander 1964). Hereafter "display" will refer to the head-down display and "cowbird" will refer to the Brown-headed Cowbird.

The function of the head-down display has been explained by a number of authors in sometimes contrasting ways. The purpose of this study, therefore, was to summarize explanations of the display in the form of four hypotheses and to evaluate those hypotheses using data from free-ranging and captive cowbirds.

Hypothesis 1.—The display is an adaptation for brood parasitism, which functions in reducing host species' aggressive tendencies toward a cowbird so that the cowbird can remain on the host's territory and/or approach the host's nest with less opposition (Selander and La Rue 1961).

Hypothesis 2.—"The display is an aggressively motivated gesture that cowbirds use in a variety of contexts to assess the fighting potential of other birds, . . . to establish dominance," or to integrate social units (Rothstein 1980).

Hypothesis 3.—The display is an example of behavioral mimicry. Cowbirds deceive display recipients: the recipient interprets the display as appeasing, while the cowbird's intent is to threaten (Rothstein 1980).

Hypothesis 4.—The display is rare in nature, and, because there is a lack of recorded observations, the display has little "biological significance" (Dow 1968).

STUDY AREA AND METHODS

Free-ranging cowbirds.—The first field study was conducted near Bowling Green, Ohio, from 6 March

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until 28 April 1976. The site, a rectangular strip of land of approximately 3 ha, was bisected by a paved road and adjacent to the east bank of the Portage River (North Branch) in Wood County. Observations were recorded from a car parked 10–25 m from the river. That portion of the study site west of the road and adjacent to the river was a flood plain dominated by deciduous trees, while the portion east of the road was a cultivated field consisting of corn stubble.

The second field study was conducted in State College, Pennsylvania, from 6 January until 12 January 1981. The site included a row of forsythia bushes (*Forsythia* sp.) approximately 8 m × 18 m × 2 m. A gravel road curved around the bushes and passed within 2 m of their north end. Observations were recorded from a car parked 10–20 m from the bushes. The area surrounding the bushes was mowed grass to the east and cultivated fields of corn stubble to the west.

Behavioral interactions were observed with the aid of 7–15 × 35-mm binoculars during 59.2 h of observation between 0800 and 1830.

Captive cowbirds.—A total of 45 cowbirds (24 AHY males, 8 HY males, and 13 females) was maintained in captivity during the winter and spring of 1976. HY males (males that hatched during 1975) were distinguished from AHY males (males that hatched before 1975) by an incomplete post-juvenile molt of the humeral tract (Baird 1958, Selander and Giller 1960). All 45 birds were caught in northwestern Ohio during the late summer and fall of 1975 with modified crow traps.

Captive birds were separated by sex, housed in 1.84 m × 2.63 m × 2.31 m holding cages in a barn near Bowling Green, and exposed to the natural photoperiod via windows. The observation cage, of the same size as the holding cages, had one window and five perches. Food (50–50% mixture of cracked corn and chick starter) and water were constantly available.

Canvas covered the north wall of the observation cage, providing visual but not auditory isolation of the study group from the other captive birds in the barn. Observations were made from an opening in a burlap enclosed walkway so that the study group as well as the rest of the birds in the barn could not see the observer.

Captive cowbirds were observed in four different groups of six birds each: females, HY males, AHY males, and mixed groups (two females, two HY males, and two AHY males). Females could not be separated confidently by age and therefore were not divided into age groups. Each group type was observed for a 5-day period during 11 January–22 February and during 26 March–30 April. Observations were recorded between 0805 and 1838.

All study groups were treated identically. Birds in each group were banded with U.S. Fish and Wildlife Service bands and unique colored leg bands, then allowed to habituate to the observation cage for 5 days. Observations began on the sixth day.

The entire group was observed for 20 min, and a record was kept of the total supplants, retreats, and head-down displays for 5 days; the group was then removed and the succeeding group placed in the cage to begin its habituation period. The order of group observation was randomized.

Description of behaviors.—"Supplanting" is an agonistic behavior that occurs when one bird displaces another (Darley 1968: 20–21). Variation in supplanting can arise from the speed of approach and the sequence or amplitude of behaviors.

"Retreating" includes "any pattern, walking, hopping, or flying, used by a submissive bird to leave" (Darley 1968: 21). When a two-bird interaction resulted in one bird displacing the other, there was always at least one supplant and one retreat.

The head-down display was first described by Selander and La Rue (1961). While displaying, the cowbird's "head is bowed" so that "the bill is directed vertically downward or in toward the cowbird's body." The orientation of the cowbird's body to the recipient can either be directly toward or at an angle away from the recipient. Commonly, the cowbird will display as it approaches the recipient, ceasing its approach when it is about 2 cm away from the recipient. Occasionally, the cowbird's approach continues until it touches the recipient bird's breast with the top of its head. Like supplanting and retreating, head-down displays varied in duration, amplitude, and speed of the displayor's approach.

Data analysis.—Captive birds were ranked by social status based on their supplant and retreat records (Scott 1977). The bird that supplanted its group members most often and retreated least was ranked as the alpha bird.

Displays by free-ranging birds were compared by sex, recipient species, and supplants. Displays by captive birds were compared by social status. In Tables 2 and 3 we analyzed "display incidents" as defined by Rothstein (1977: 17).

Statistical analyses followed methods presented by Zar (1974). Sample sizes greater than or equal to 10 and less than or equal to 25 were analyzed using a binomial distribution. Samples greater than 25 were evaluated using a two-tailed χ^2 test corrected for continuity. A sample size of less than 10 was considered too small for meaningful statistical analysis.

RESULTS

Free-ranging cowbirds.—None of the recipients of displays by free-ranging cowbirds responded by displaying in return to the initiator. Recipients responded either by retreating, pecking at the displayor, supplanting the displayor, or seeming to ignore the displayor. None of the recipients preened conspecifics.

Table 1. Head-down displays performed by free-ranging Brown-headed Cowbirds in northwestern Ohio and central Pennsylvania.

Sex of displaying cowbird	Recipient species	Number of displays	Number of displays where recipient preened cowbird	Supplants by Cowbird	Supplants by Recipient
	A. Ohio observations (54 h during 33 visits, 0820–1830, 6 March–28 April 1976)				
Female	♀ House Sparrow	6		5	1
	♂ House Sparrow	2		2	
	♀ Red-winged Blackbird	54	12	21	4
	♀ Rusty Blackbird	2		1	
	♀ Brown-headed Cowbird	1			1
Male	♂ House Sparrow	1		1	
	♀ Red-winged Blackbird	10		6	
Ohio Total	4 species	76	12	36	6
	B. Pennsylvania observations (5.2 h during 5 visits, 1125–1610, 6 January–12 January 1981)				
Female	♀ House Sparrow	23	2	12	
	♂ House Sparrow	30		9	2
Male	♀ House Sparrow	52		37	4
	♂ House Sparrow	104	11	74	1
	♀ Brown-headed Cowbird	2		1	
	♂ Brown-headed Cowbird	1			
Pennsylvania Total	2 species	212	13	133	7
Grand Total	4 species	288	25	169	13

Free-ranging cowbirds performed 288 head-down displays during 38 visits to the study sites that totalled 59.2 h of observation (Table 1). Cowbirds presented displays to four species: female Red-winged Blackbirds (*Agelaius phoeniceus*), a female Rusty Blackbird (*Euphagus carolinus*), male and female House Sparrows (*Passer domesticus*), and male and female cowbirds (Table 1).

All but two recorded displays were observed while cowbirds were roosting during daylight hours in trees or shrubs in mixed-species flocks adjacent to the feeding areas of corn stubble or stockyard. The remaining two displays were performed by cowbirds in Pennsylvania while on snow-covered ground.

Some displays were seen in rapid succession, separated by about 1–5 s. The birds performing these successive displays quickly followed and repeatedly displayed toward the recipient if the recipient remained in place or hopped or flew a short distance away ($\leq$1 m). If the recipient bird flew a longer distance away, the cowbird either displayed toward another bird or stopped displaying altogether. As a result of these successive displays, the head-down display appeared to be more clumped than evenly spread out in time. If display rate is considered, based upon the number of minutes that cowbirds were present, a display was observed every 42.6 min in Ohio and every 1.5 min in Pennsylvania.

Female cowbirds in Ohio displayed more often than males (65 times vs. 11 times, $P \leq 0.001$; Table 1), though maximum estimates of males ($n = 338$) and females ($n = 333$) observed were nearly equal. Male cowbirds displayed more often than females in Pennsylvania (159 times vs. 53 times, $P \leq 0.01$; Table 1); maximum estimates of males ($n = 125$) and females ($n = 46$) showed that males predominated.

Eighty-six percent of female cowbird displays and 91% of male cowbird displays in Ohio were directed toward female Red-winged Blackbirds ($P \leq 0.001$ in both cases; Table 1). Other passerines such as male Red-wings, European Starlings (*Sturnus vulgaris*), Common Grackles (*Quiscalus quiscula*), Northern Cardinals (*Cardinalis cardinalis*), and Song Sparrows (*Melospiza melodia*) were commonly observed at the Ohio site and appeared to be available

Table 2. Head-down displays performed by captive cowbirds during 1976. Each group was observed for five 20-min periods. Matrices are arranged with the alpha bird in the top left corner and progressively subordinate birds to the right and below the alpha bird. Because no displays were observed in the group of six AHY ♂ (16 April–20 April), no matrix is included for that group. Recipients are listed horizontally, displayors vertically.

6 AHY ♂ (16 Feb–20 Feb); mutual displays = 14

	C	A	E	B	D	F	Σ
C	—	2	0	1	4	4	11
A	0	—	0	0	0	0	0
E	0	0	—	0	0	14	14
B	0	0	0	—	0	0	0
D	0	0	0	0	—	16	16
F	2	0	0	0	6	—	8
							Σ = 49

5 ♀ (11 Jan–15 Jan); mutual displays = 3

	E	C	A	D	B	Σ
E	—	0	2	0	0	2
C	0	—	1	0	1	2
A	0	1	—	1	0	2
D	0	0	0	—	0	0
B	0	0	0	0	—	0
						Σ = 6

6 HY ♂ (6 Apr–10 Apr); mutual displays = 7

	D	H	G	B	C	F	Σ
D	—	0	0	2	6	1	9
H	0	—	0	0	0	0	0
G	0	0	—	0	0	2	2
B	0	0	0	—	0	0	0
C	3	0	0	0	—	0	3
F	0	0	0	0	0	—	0
							Σ = 14

2 AHY ♂, 2 HY ♂, 2 ♀ (4 Feb–8 Feb); mutual displays = 7

	AHY♂	HY♂	HY♂	AHY♂	♀	♀	
	N	F	C	O	C	E	Σ
N	—	0	0	0	0	0	0
F	0	—	0	0	4	0	4
C	0	0	—	0	0	1	1
O	0	0	0	—	0	0	0
C	0	0	0	0	—	7	7
E	0	0	0	0	1	—	1
							Σ = 13

6 HY ♂ (23 Jan–27 Jan); mutual displays = 23

	D	B	E	A	C	F	Σ
D	—	0	0	0	0	0	0
B	3	—	0	0	17	5	25
E	0	1	—	3	0	0	4
A	0	0	0	—	0	2	2
C	0	0	0	0	—	0	0
F	0	0	0	0	0	—	0
							Σ = 31

2 AHY ♂, 2 HY ♂, 2 ♀ (4 Feb–8 Feb); mutual displays = 83

	HY♂	HY♂	AHY♂	AHY♂	♀	♀	
	H	G	H	G	G	F	Σ
H	—	1	0	0	0	4	5
G	0	—	0	0	3	16	19
H	0	0	—	9	0	37	46
G	0	0	0	—	0	1	1
G	0	0	0	0	—	13	13
F	0	2	6	0	0	—	8
							Σ = 92

6 ♀ (26 Apr–30 Apr); mutual displays = 48

	G	E	C	D	A	B	Σ
G	—	0	12	0	0	0	12
E	0	—	11	0	2	0	13
C	1	7	—	1	1	1	11
D	0	2	0	—	1	2	5
A	5	0	3	10	—	6	24
B	1	1	1	3	14	—	20
							Σ = 85

in time and space for cowbirds to display toward if they had chosen to do so.

In Pennsylvania, where only cowbirds and House Sparrows were observed, House Sparrows were recipients of 209 of 212 displays (Table 1). Male and female House Sparrows were present in approximately a 1:1 ratio. House Sparrows outnumbered cowbirds during all days of observation; estimates of the number of birds present per visit varied from 18 to more than 150 for House Sparrows and from 5 to 75 for cowbirds. Male cowbirds displayed more often toward male House Sparrows ($P \leqslant 0.001$) than toward female House Sparrows (Table 1).

Female Red-wings in Ohio and male and female House Sparrows in Pennsylvania were the

TABLE 3. Summary of two-tailed χ^2 analysis of head-down displays performed by dominant versus subordinate captive cowbirds.

Group type, age, and sex of displaying cowbird	Dominance position of birds that performed display most often[a]: Jan–Feb observation period	March–April observation period	Total
Segregated AHY ♂♂	—	—	—
Segregated HY ♂♂	top	top	top
Segregated ♂♂	top	top	top
Segregated ♀♀	sm[b]	—	—
Segregated ♂♂ + ♀♀	top	—	top
Mixed ♂♂ + ♀♀	top	—	top
Total	top	—	top

[a] Top denotes that the top three birds (top two for females Jan–Feb segregated group) in the dominance hierarchy performed the display more often ($P \leq 0.05$) than subordinates.

[b] Sample size was <10 and therefore not tested.

only birds observed responding to the head-down display by preening the feathers of the displaying cowbird. These birds preened male and female cowbirds on the cowbirds' capital tracts and/or the backs of their necks during 25 of 288 displays (9%; Table 1).

Preening seemed to be a strong stimulus for subsequent displaying at both sites, as a cowbird that had been preened seemed more quickly and more persistently to pursue and display toward the bird that had preened it. In Pennsylvania, we tested this prediction by recording displays performed by birds that had just been preened versus those birds that had not been preened but that had displayed within the previous 5 min. The birds that had been preened displayed far more often than those that had not been preened ($P \leq 0.001$); two birds that had just been preened displayed 29 times during the 3.5 min that we could follow them, while three birds that had not been preened displayed 33 times during 15.5 min.

Displaying cowbirds in both Ohio and Pennsylvania supplanted recipients more often ($P \leq 0.001$) than they retreated from recipients (Table 1). Following a supplant, displaying cowbirds were often observed to continue their approach toward the recipient, which had moved a short distance away. Frequently, this sequence of behaviors was repeated, resulting in a series of supplants by the displayor. When recipients supplanted a displaying cowbird, it was done most often by pecking. Eight of 17 pecks by recipients toward displaying females were associated with the retreat of the displaying female.

Captive cowbirds.—A total of 475 intraspecific displays by captive birds was recorded during 13.3 h of observation (Table 2). Head-down displays were observed in all groups during both observation periods except AHY males from 16 April until 20 April; they were not observed performing any displays.

Captive cowbirds, in all groups and during both observation periods, exhibited a peck dominance hierarchy, and females were subordinate to males (see Scott 1977: 25–26 for dominance data). Using the term dominant to refer to the top three birds in the dominance hierarchy (top two for females Jan-Feb segregated flock) and subordinate to refer to the bottom three birds in the hierarchy, we found that when there were differences in display frequencies, dominant birds always performed the display more often ($P \leq 0.05$) than subordinates (Table 3). Differences in favor of dominant birds were observed more often during the first observation period than during the second.

DISCUSSION

Hypothesis 1.—Our study, as well as other evidence, supports the appeasement portion of hypothesis 1. We observed recipients preening free-ranging cowbirds during 25 of 288 displays (Table 1). Interspecific preening was not observed in any other context. Similarly, it was not uncommon for captive birds to contact each other during a mutual display. Thus, displaying birds, both free-ranging and captive, were able to get close enough to recipients to make physical contact for periods of time up to 2 min, something that was not observed in any other context.

Similarly, Stevenson (1969) concluded after observing 2,530 displays by captive cowbirds that the display allows birds to approach recipients more closely than if they were not displaying. Results from our study support Stevenson's conclusion.

In addition, Selander and La Rue's (1961) study showed that during interspecific displays, recipients most often initially responded by pecking at the displaying cowbirds but, after additional exposure to the display, gradually began to peck less and preen more. Allopreening was considered less aggressive than pecking. Robertson and Norman (1976) in their field study with mounted birds also showed that the display appeases; potential hosts were less aggressive to mounts in the display posture than mounts in the "normal" posture. Finally, Lowther and Rothstein (1980) suggested that displays performed by cowbirds less than 1.5 months of age may function in appeasement.

We found no evidence during our field observations that the display and brood parasitism are directly associated. The possibility that it is infrequently performed in that context, however, cannot be ruled out by this study. Displays performed by free-ranging birds and observed during this study were directed toward species that are uncommon hosts of the cowbird (Friedmann 1929, Hicks 1934, Scott unpubl. data). Friedmann (1963) and Rothstein (1980) also state that the display is seldom directed toward common hosts.

Observations and conclusions by other authors similarly fail to support the parasitism component of hypothesis 1. Mayfield (1961) and Friedmann (1963) state that at the time when female cowbirds lay their eggs, small passerines are not apt to be present at their nests. Hence, female cowbirds in the process of egg laying would not commonly interact with potential hosts. Hann (1937, 1941), Mayfield (1961), and Norman and Robertson (1975) observed female cowbirds "inspecting" potential host nests before cowbird egg laying took place. No cowbird behavior was reported that could be interpreted as a head-down display. Though Prescott (1947) observed an instance when a female cowbird approached a Red-eyed Vireo (*Vireo olivaceus*) sitting on its nest and Hann (1937) observed the same with Ovenbirds (*Seiurus aurocapillus*), the cowbirds supplanted the vireo and Ovenbirds without performing a behavior that could be interpreted as a head-down display. In fact, the cowbird observed by Prescott supplanted the vireo with a "distinct pecking motion."

Frequency of the display does not appear to be influenced by hormone production in males (Selander and La Rue 1961). Assuming that the display is directly involved in brood parasitism, one could predict that the frequency of the display would increase during the breeding season concomitantly with increasing hormone production. Selander and La Rue (1961), however, did not observe variation in the rate at which their captive male cowbirds displayed during mid-April following bilateral castration in January.

Displays performed by other species of cowbirds suggest that the display may not have evolved in a direct relationship with brood parasitism. Selander (1964) suggests that the Bay-winged Cowbird's (*Molothrus badius*) "preening invitation display" is an evolutionary precursor to the head-down display of the more evolutionarily specialized Brown-headed Cowbird. The Bay-winged Cowbird is not a brood parasite (Friedmann 1929). Hence, the display may have evolved before the habit of brood parasitism.

Hypothesis 2.—Two aspects of hypothesis 2 were supported by this study. Patterns of displaying were observed that support the display's involvement in integrating social units (Rothstein 1977). For example, birds in the top half of the dominance hierarchy displayed more often than birds in the bottom half ($P \leq 0.05$; Table 3). In addition, when differences in display rates existed in comparisons between segregated groups and the corresponding age or sex class of mixed groups, birds displayed more often ($P \leq 0.01$) when both sexes were present than when just one sex was present (Table 2). The only exception to this trend was that females in the segregated flock during March-April displayed more often than females in the mixed flock. It also appeared from the study of captive birds that a displayor may be assessing the agonistic tendencies of the recipient, especially when cowbirds first interact with an unfamiliar individual (Rothstein 1980). This appeared to be true following the introduction of House Sparrows and additional cowbirds to the observation cage (Scott unpubl. data).

We do not agree with that portion of hypothesis 2 that describes the display as a threat. Rothstein concluded "that the display's true message is threat" (Rothstein 1980: 157), because dominant captive birds display more often than their subordinates and because some displaying captive birds alternately displayed and pecked. We take issue with this conclusion for two reasons. First, it was not disproven that dominants may display toward subordinates in order to appease them. That dominant birds display most often to subordinates does not clearly indicate that the display is aggressive. Dominant birds, free-ranging or captive, may display most often toward subordinates in order to get and stay close to subordinates, not to threaten them. For example, among captive birds dominant males may display toward subordinate females in order to stay close to them. We, as well as Stevenson (1969), interpret no clear intent by displaying cowbirds to displace recipients. On the contrary, based on the frequent observation that displaying free-ranging and captive cowbirds persistently pursued fleeing recipients, it seemed to us that displaying cowbirds "wanted" recipients to remain in close proximity. We discussed under hypothesis 1 additional reasons why the display is appeasing. Second, the conclusion that pecking and displaying have the same meaning for cowbirds simply because their performances are closely associated in time is not necessarily valid.

Rothstein's (1980) results show that the display is performed by captive birds in a situation of conflict. Observations during this study agree. Such a context may explain why some cowbirds alternately displayed and pecked. Because we interpreted the display to be non-aggressive, appeasing, and performed in a situation of conflict, we prefer to refer to it as a complex agonistic behavior, i.e. "any behavior associated with conflict or fighting between two individuals," (Scott 1956: 214–215) rather than as an aggressive behavior.

Rothstein (1977, 1980) defined the situation of conflict as the violation of another bird's individual distance. The only thing that we thought could be threatening about the display was the displayor's close proximity to the recipient, not the displayor's posture or movements.

Rothstein's (1980) experiments also show that the display is most often performed by birds that are dominant to recipients. Observations during this study support that conclusion.

Our results show that among captive birds males were dominant to females (Table 2) and that females, across observation periods and while in mixed groups, responded to 66 displaying males by displaying in return 58 times. If cowbirds display in order to dominate other birds and the display is a threat, we would not expect that a subordinate female, who seldom threatens males with recognized cowbird threat behaviors (Scott 1977), would commonly return the head-down display of a dominant male as was observed in our study. Furthermore, it is not clear why such a complicated threat behavior would be selected for when other threats, like bill pointing or pecking, would seem to displace and dominate a subordinate recipient more quickly than would a head-down display.

Rothstein (1980) explains mutual displays, like those above, as a "test of wills" or, alternatively, as mutual threats by individuals of similar social status. Although mutual displays could be mutual threats by birds of similar status, in this study subordinate females and dominant males commonly displayed mutually. Our observations, therefore, show that the prediction that mutually displaying birds are of similar social status frequently is not true.

Hypothesis 3.—The display cannot be behavioral mimicry, because there is no model for cowbirds to mimic. Suggesting that the display is an example of behavioral mimicry implies that there is selective pressure on cowbirds to mimic intraspecific behaviors of recipient species. No field-verified model behavior was proposed with the mimicry theory, nor have we seen during hundreds of hours in the field a behavior performed intraspecifically by recipient species that might be interpreted as a model for the display. Furthermore, the mimicry theory does not explain what specific selective advantage(s) a displayor gains by mimicking the behavior of another species.

As an alternative to the behavioral mimicry theory, we propose a simpler, more straightforward explanation: both displayor and recipient interpret the display as appeasement. Even if additional investigation substantiates the more complex deception/aggression hypothesis (Rothstein 1980) and it is shown that "receivers do not respond to the true message being sent" (Rothstein 1980: 173), the display should not be labeled as behavioral mimicry. Not all forms of deception constitute mimicry.

Hypothesis 4.—Hypothesis 4 is refuted by our observations of free-ranging cowbirds. We observed the display 288 times during 59.2 h of field observation (Table 1). Furthermore, the widespread occurrence of the display is supported by the geographical variation in its sightings. We have observed the display in Connecticut, Maryland (unpubl. data), Ohio, and Pennsylvania. Lowther and Rothstein (1980) reported it in Kansas; Rothstein (1980) saw it in California, Connecticut, and New York; Dow (1968) observed it in Tennessee; and Darley (1968) saw it in Ontario. Selander and La Rue (1961) have sightings from Texas, Rhode Island, New York, Oklahoma, and Florida.

If more observations were undertaken of cowbirds as the birds roost during the day in mixed-species flocks adjacent to feeding areas, it would become apparent that the display is performed often by free-ranging cowbirds. Rothstein (1977, 1980) previously reported cowbirds displaying in this context; observations during this study support the context and provide additional details.

Incorporating those aspects of hypotheses 1–4 that were not rejected, we propose a consolidated hypothesis for the function of the head-down display as follows:

> The head-down display is an appeasing, agonistic behavior that reduces agonistic behaviors of the recipient toward the displaying cowbird. The displayor is generally dominant to the recipient, and preening is a stimulus for subsequent displaying by the preened cowbird. The display functions in: (a) obtaining food, (b) minimizing roosting energetics, and/or (c) establishing flock order.

For the display recipient, preening could be a "conflict behavior performed" toward cowbirds who have violated the recipient's individual distance (Rothstein 1971, 1980). For cowbirds, preening appears to be important to the display's appeasement function. Pennsylvania cowbirds that had just been preened displayed more often than those that had not been preened ($P \leq 0.001$). Moreover, cowbirds may display toward female Red-wings or House Sparrows most often, because the probability of being preened is greatest with those birds. Field observations during this study suggest that preening is a positive response to the displayor that might signal that the agonistic tendencies of the recipient have been reduced. In this way, the displayor may be assessing agonistic tendencies, as Rothstein (1980) has proposed.

The hypothesized display functions are speculative. Although we will discuss them separately, they are not necessarily mutually exclusive and may or may not operate in concert.

Selander and La Rue (1961) were the first to speculate briefly about the feeding and roosting functions of the head-down display. Joining a foraging group may be advantageous for a cowbird in obtaining food (Ricklefs 1973: 226). The head-down display may facilitate a cowbird's joining a foraging group by appeasing flock members or by helping to assess agonistic tendencies of flock members. In addition, the display may help a cowbird position itself in roosting trees where overnight energy expenditure for thermoregulation would be minimized. Lustick and Kelty (1979) have shown that location in roosting trees affects thermoregulation by Starlings and blackbirds. In a study of a winter roost in Texas (Johnson et al. 1980), researchers found that cowbird mortality was positively associated with freezing temperatures and "depletion of winter food supplies." Because feeding and roosting are often flock activities for cowbirds (pers. obs.), the display may placate other bird species with whom cowbirds flock, thereby facilitating the cowbirds' inclusion in the flock.

Rothstein (1980) suggested the flock-order function for the head-down display. It has long been known that disorganization of bird flocks can result in negative effects on individuals within the flock (Guhl and Alee 1944). Social disorganization could occur, especially when cowbirds are first captured and placed in a cage with unfamiliar individuals, because the birds are unnaturally overcrowded in their cage (Emlen 1950). Rothstein (1977) has stated that for captive cowbirds the number of intra- and interspecific displays decreased rapidly after birds had been maintained in intact groups for 2–5 months. Perhaps the display is observed less often among birds that have been together for a long time because social order has been established and group agonistic interactions have, therefore, become less frequent. In this captive setting, an appeasement display could benefit a dominant bird by reducing agonisitic behaviors from conspecifics and allowing more time for behaviors that are more productive than fighting (like feeding), by allowing males to remain close to females, or by providing cowbirds with an assessement of the agonistic tendencies of other flock members (Rothstein 1980).

The flock-order function of the display for free-ranging birds may operate as follows. Free-ranging cowbirds might display most often interspecifically toward species with whom they flock because interspecific flocking is important to their survival (e.g. for food gathering, roosting-site location, or predator avoidance) and the head-down display reduces the disorganizing effects of a cowbird joining a mixed-species flock. Because interspecific relationships are more fragile and more easily broken off than intraspecific ones (Scott 1975), the display may have evolved into a behavior that fosters important interspecific relationships.

To the best of our knowledge it is not known whether or not particular free-ranging cowbirds display most often or whether or not those birds are intraspecifically dominant, a trend that has been observed among captive cowbirds (Table 3). If this trend were verified for free-ranging cowbirds, our hypothesis would predict that dominant, free-ranging birds display most often because the display allows them to remain close to birds with which they flock, which in turn leads them to feeding or roosting sites, helps in avoiding predators, and/or provides assessment of the agonistic tendencies of flock members.

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TIME AND ENERGY BUDGETS OF THE MOCKINGBIRD (*MIMUS POLYGLOTTOS*) DURING THE BREEDING SEASON

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Abstract.—A time and energy budget of male and female Mockingbirds (*Mimus polyglottos*) in six phases of their breeding cycle was completed using the equivalent temperature model to predict perching metabolic rates. Recorded time-budget behaviors included perching, bipedal locomotion, flight, and the time spent in the sun and shade. Over the total study period, males and females spent an average of 92.3% and 92.8% of their active day perched, 2.4% and 1.6% in bipedal locomotion, and 5.3% and 5.6% in flight, respectively. BMR plus thermostatic requirements averaged, seasonally, 78.1% of DEE_{tot} in males and 76.1% in females. The choice of shaded or exposed microhabitats made very little difference in energy expenditure. DEE_{tot} varied from 96.9 kJ in males with incubating females to 113.0 kJ in males caring for fledglings, and from 75.1 kJ in incubating females to 113.2 kJ in females caring for fledglings. Unmated, pre-nest-building, and incubating birds spent significantly less energy than did birds caring for nestlings ($P < 0.05$) or birds caring for fledglings ($P < 0.05$). With the exception of the nest-building phase, when females are producing eggs, and the incubation phase, when females gain insulation from the nest, male and female DEE_{tot} closely paralleled each other throughout the season. The large amount of predation that occurred at the study site suggests that birds may allocate time to perching to minimize the probability of predation on themselves or their offspring. *Received 26 February 1982, accepted 4 October 1982.*

A viable approach to ecological and evolutionary problems is available through the use of time- and energy-budget analysis. Because time and energy are resources common to all organisms, this approach can serve both to quantify the diversity of interactions between an organism and its environment (a functional problem) and to decipher evolutionary trends and their causes (Porter and Gates 1969, King 1974). This is the key to the vitality of the approach: functional and evolutionary problems can be addressed simultaneously (Mayr 1961). As more comparative time and energy data are gathered and analyzed, ecological and phylogenetic correlates of life history elements (e.g. energy invested per egg, energy invested in offspring, time and energy devoted to offspring by males and females) will emerge, increasing our power to discriminate ecological problems and the modes in which natural selection attempts to solve them. But this is not all that the technique does for us. When we enter the Hutchinsonian "ecological theater" (Hutchinson 1965) armed with time and energy concepts, we come out with a more thorough understanding of the proximal elements linking organisms to their environments. We become sensitive to the energetic patchiness of an organism's environment and may visualize it as a series of microhabitats in which biological and physical factors interact to determine whether an organism experiences net energy gains or losses. We are granted a clearer understanding of the reasons for the distribution of organisms within habitats.

The habits of the Mockingbird (*Mimus polyglottos*) make it an ideal species of which to analyze time and energy budgets. Individuals nest in semi-open habitats, which facilitates behavioral observations; they are highly territorial; and their home ranges are sufficiently small that they can be covered rapidly by a person on foot. In this report I present time and energy budgets for Mockingbirds during a single breeding season in Davis, California. The major goals were to discern the dynamics of time and energy expenditure of males and females throughout the reproductive cycle, to investigate the role that microhabitat selection

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plays in determining energy expenditure, and to compare the time budgets of this Mockingbird population with those collected by Utter (1971) on Mockingbirds in New Jersey.

METHODS

The activity patterns of Mockingbirds were studied in riparian and urban habitats near the veterinary medical complex of the University of California at Davis, Yolo County, California. The study lasted from 2 February 1978 to 6 June 1978. The habitat of most birds consisted of fallow fields with patches of asphalt parking lots and expanses of lawn. Oaks (*Quercus ilex* and/or *Quercus agrifolia*) were scattered over most birds' home ranges. Pyracanthaberry (*Pyracantha* sp.) was commonly available, and its fruits were used by birds in all phases of the breeding cycle.

Five Mockingbirds were mist-netted, weighed, and color-banded in January 1978. The sexes of the birds were determined by subsequent observations of behavior (singing, displays, etc.). The mean weight of the birds was 54.8 g (range, 48.9–59.3 g). The only positively identified female in the sample also weighed 54.8 g, so I assume that there is no weight dimorphism.

The duration of three types of activities and the time spent in the sun and in the shade were quantified using a panel of four stopwatches. Data were primarily recorded in hourly periods. At the end of each hourly period, air temperature and the percentage of cloud cover were recorded, and windspeeds were measured in the sun and shade in microhabitats similar to the ones that the bird had occupied. Windspeed was measured with a Thermonetics series 100 hot wire anemometer. Data on total short-wave radiation per hour were obtained from the meteorological station at the University of California at Davis, located 400 m from the study site.

Activity categories included perching, flying, and bipedal locomotion. Bipedal locomotion (*BPM*) was restricted to the actual moments when locomotion occurred. The *BPM* category does not represent time spent foraging. The open habitat allowed me to monitor the birds' behaviors continuously. In the rare instances that birds were lost during observation periods, the data for that period were excluded unless visual contact was regained in less than 2 min.

The birds' seasonal cycle was divided into six data-collection phases: unmated, pre-nest-building, nest-building, incubation, nestling care, and fledgling care. Data were collected throughout the day and several times at night. Male and female power-consumption data were pooled in each phase for statistical analysis.

Home ranges were estimated from behavioral observations several times during the study. Home ranges were traced on scale photographs (1″ = 100′) obtained from the Department of Architects and Engineers at the University of California at Davis. Areas were then calculated from these photographs.

CALCULATION OF ENERGY EXPENDITURE

An energy budget for an animal under steady-state conditions with its environment, where conduction is not important, can be written

$$MR - \lambda E = [\rho c_p/(r_b + r_e)](T_b - T_e) \qquad (1)$$

where MR is metabolic rate ($W \cdot m^{-2}$), λE is latent heat loss ($W \cdot m^{-2}$), r_b is whole-body thermal resistance ($s \cdot m^{-1}$), r_e is equivalent resistance, T_b is body temperature (°C), T_e is equivalent temperature, and the product of the density (ρ) and the specific heat of air (c_p) is a constant ($1{,}200\ J \cdot m^{-3} \cdot K^{-1}$ at 20°C) (Mahoney 1976, Campbell 1977). This equation was used to predict the metabolic rates of perching Mockingbirds during their activity phase whenever environmental conditions were such that MR exceeded the metabolic rate predicted by the Aschoff and Pohl (1970) (A/P) diurnal equation for passerines, multiplied by a factor of 1.2 [the factor 1.2 corrects for illumination under diurnal conditions (Mahoney and King 1977)]. Such conditions existed when $35°C \leqq T_e \leqq 14°C$.

To compute a metabolic rate with equation 1, it is necessary to measure or calculate values for several bird and environmental parameters. Environmental parameters include short-wave (SW) radiation, long-wave (LW) radiation, windspeed, and ambient temperature. A bird's SW radiation environment was determined from measured values of total SW radiation using the technique of Campbell (1977: table 5.1, equations 5.7 and 5.8; 1981: equations 1.5, 1.6, 1.9). The LW radiation environment was calculated from equation 11 in Unsworth and Monteith (1975) and equation 5.13 in Campbell (1977). Bird parameters incorporated in equation 1 include the characteristic dimension (d), the SW absorptivities of the back and belly, the amount of area exposed to different types of SW radiation, various resistances to heat transfer, and evaporative water loss. The characteristic dimension was measured, and the absorptivities of the birds' backs and bellies (0.6 and 0.51, respectively) were estimated by comparing Mockingbird plumage to bird plumages that were similarly colored and the absorptivities of which were known. The ratio of the area exposed to perpendicular SW radiation over the total area of the bird was estimated as 0.21 (Mugaas 1976). It was also assumed that the upper half of the bird's total area was exposed to scattered SW radiation, while the lower half was exposed to reflected SW radiation (Mahoney 1976). Maximum total resistance was calculated from $r_t = 283m^{0.21}$, where m is the bird's mass (g) (Robinson et al. 1976). The maximum value that r_e could attain was 158 $\mathrm{s \cdot m^{-1}}$ or 24% of the maximum total resistance (Mahoney and King 1977). Maximum body resistance, r_b max, during the day was calculated to equal 423 $\mathrm{s \cdot m^{-1}}$ by equations given in Robinson et al. (1976). Using this value as a peak for r_b and the shape of Fig. 2 in Mahoney and King (1977), I derived body resistances at other equivalent temperatures. Evaporative water loss (E) was calculated from data from the Pyrrhuloxia (*Cardinalis sinuatus*) and the Northern Cardinal (*C. cardinalis*) (Hinds and Calder 1973). They give an equation for water loss between 20°C and 32.5°C: E(g/day)= $0.48m^{0.545}$, where m is body mass (g). This equation was used to calculate evaporative water loss in the range of 20°C–32.5°C. Below 20°C, the graph was drawn to 0.5% body mass evaporated per hour at 13° C (in accordance with their data) and then was further extrapolated to 7° C, the lowest T_e that occurred during my study. At 45°C the data of Hinds and Calder give unreasonably low results for a Mockingbird's total metabolic rate. For this reason, I assumed that evaporative water loss is equivalent to metabolic heat production at an equivalent temperature equal to the birds' body temperature (42°C), and I set both equal to 105 $\mathrm{W \cdot m^{-2}}$ at this temperature. For equivalent temperatures greater than 35°C, this approximation yields the following equation: E $(\mathrm{W \cdot m^{-2}}) = 10.2\ T_e(^\circ\mathrm{C}) - 324.2$.

Calculation of hourly metabolic rates.—Two equivalent temperatures were determined for each observation period: one for conditions of full sunlight and one for conditions in the shade. A metabolic rate was determined for each equivalent temperature. The metabolic rate was then recalculated to represent the proportion of each hour spent in the sun and shade.

The costs of bipedal locomotion and flight were considered to be independent of environmental conditions. The cost of bipedal locomotion (*BPM*) was assumed to be 1.5 times the cost of perching in the thermal neutral zone, and the cost of flight was calculated as equal to 9.4 times the metabolic rate calculated from the Aschoff and Pohl (1970) equation for passerines resting at night (Hart and Berger 1972).

The final cost of an hourly period for a nonreproducing bird was the sum of the cost of each behavior ($\mathrm{J \cdot m^{-2} \cdot h^{-1}}$), times the fraction of the hour spent in that behavior, multiplied by the surface area of the bird ($\mathrm{m^2}$). Plumage surface areas were determined from $SA = 7.81(m)^{0.667}$ (Walsberg and King 1978a), where m is bird mass (g) and SA is surface area ($\mathrm{cm^2}$).

Nighttime energy expenditure.—Hourly nighttime energy expenditure in the thermal neutral zone (TNZ) (22.5–35°C) was calculated from $114.8\,M^{0.726}$ (M in kg) (Aschoff and Pohl 1970). The range of environmental temperatures that delimits the TNZ was calculated for the lower critical temperature from $T_{LC} = T_b - 6.98m^{0.266}$, where m is mass (g) (Calder and King 1974). The upper critical temperature was assumed to equal 35°C. Because no windspeed or LW radiation data were collected at night, when temperatures dropped below the TNZ, Kendeigh's (1969) equation, H (kcals/day) = $4.769m^{0.417}$ [where m is mass (g)], was used to calculate a metabolic rate at 0°C, and metabolism was computed based on the assumption that it decreases linearly as temperature increases from 0 to 22.5°C. A single temperature (the mean nighttime temperature) was used to calculate hourly energy expenditure.

Incubating birds.—The modeling procedure for incubating birds was the same as for nonincubating birds except for periods when birds were on the nest. Because birds nested in heavy vegetation where little or no light penetrated, SW radiation fell to 0 $\mathrm{W \cdot m^{-2}}$ under these conditions. The model assumed that 10% of the incubating bird's surface area was covered by the brood patch, that 40% of its surface was exposed, and that 50% of its surface area was in the nest (excluding the brood patch). The resistance for a 1.9-cm-wide egg (Bent 1948) was set at 41.9 $\mathrm{s \cdot m^{-1}}$; the brood patch resistance was set equal to 45 $\mathrm{s \cdot m^{-1}}$; body resistance was approximated as 423 $\mathrm{s \cdot m^{-1}}$ (max. night); and nest resistance was set equal to 300 $\mathrm{s \cdot m^{-1}}$ (values estimated in the manner of Walsberg and King 1978b). The characteristic dimension for the nest with the bird was approximated as 15 cm. All other facets of this model were similar to the analysis by Walsberg and King (1978b). In this phase of the cycle, the calculated metabolic rates for birds on the nest during the day were compared to the Aschoff and Pohl (1970) resting equation. If predicted metabolic rates on the nest during the day dropped below this value, they were set equal to it. During the night, incubating birds' metabolic rates were set equal to 82% of a nonincubating bird's metabolic rate under similar temperature conditions (Walsberg and King 1978b).

Egg formation.—Egg formation was assumed to take 5 days, and the cost of forming 1 g of egg, at an efficiency of 70%, was estimated as 6.28 kJ (King 1973). Because a single Mockingbird egg weighs 3.75–4.25 g (Hanna 1924), a total cost of 25.1 kJ per egg was assumed. Because clutch size near Davis ranged from 3 to 4 eggs ($n = 8$), the total costs to form 3 eggs in 7 days and 4 eggs in 8 days were both calculated. I chose the mean of these two values, 468 $\mathrm{J \cdot h^{-1}}$, to add to the hourly expenditure of egg-producing females. Nest-building females were the only group of birds to have this cost of production added to hourly expenditure.

Converting hourly data to daily energy expenditure.—To convert energy expenditure per hour to daily energy expenditure (DEE_{tot}), a mean value of hourly expenditure was calculated for each bird in that particular phase, and then a mean of these means was calculated. This value was used for a bird during waking hours (from 15 min before civil twilight in the morning to 15 min after civil twilight in the evening). DEE_{tot} includes the costs of basal metabolism,

TABLE 1. Sensitivity of DEE_{tot} to errors in model parameters at T_a = 10°C, T_g = 12°C.[a]

Variable[b] and % change	Radiation ($W \cdot m^{-2}$) and windspeed ($m \cdot s^{-1}$)			
	50, 0.5	880, 0.5	50, 5	880, 5
Mass				
+10%	+5%[c]	+5%	+5%	+5%
−10%	−5%	−5%	−5%	−5%
Perching[d]				
+25%	+21%	+21%	+21%	+21%
−25%	−21%	−21%	−21%	−21%
Flight[e]				
+25%	+4%	+4%	+4%	+4%
−25%	−4%	−4%	−4%	−4%
Surface area				
+25%	+7%	+2%	+8%	+8%
−25%	−6%	−5%	−9%	−6%
r_b				
+25%	−2%	−1%	−5%	−2%
−25%	+9%	+2%	+11%	+11%
Night metabolism				
+10%	+4%	+4%	+4%	+4%
−10%	−4%	−4%	−4%	−4%

[a] Values given are the percentage increase or decrease in DEE_{tot} due to the change in the parameter indicated, under the total short-wave radiation and windspead conditions specified.

[b] Other variables tested and their deviations included T_a ± 1°C; T_g ± 10°C; T_b ± 2°C; albedo, A_p/A_t, A_H/A_t, d, E, r_e, and the cost of *BPM*, all varied by 25%; and back and belly absorptivities ± 10%. All variations led to less than a 2% change in DEE_{tot}.

[c] The standard DEE_{tot}'s for the conditions of total short-wave radiation and wind given are 50, 0.5: 108.2 kJ; 880, 0.5: 107.1 kJ; 50, 5: 112.3 kJ; and 880, 5: 108.8 kJ.

[d] Costs include *BMR* plus *TR* and encompass the total 24-h period.

[e] Costs include *BMR*.

TABLE 2. Sensitivity of DEE_{tot} to errors in model parameters at T_a = 25°C, T_g = 27°C and T_a = 30°C, T_g = 32°C.[a]

Variable[b] and percentage change	Estimated DEE_{tot} ($kJ \cdot h^{-1}$)	Percentage deviation from original estimate
Mass + 10%[c]	117.2	+ 6%[d]
Perching cost + 25%[c]	124.3	+13%
Flight cost + 25%[e]	115.9	+5%
Surface area + 25%	116.4	+5%
Nighttime metabolism + 10%	113.6	+3%

[a] Under all radiation ($W \cdot m^{-2}$) and windspeed ($m \cdot s^{-1}$) conditions specified, the results were identical.

[b] Variables tested were identical to those at T_a = 10°C. All other variables led to less than a 2% change in DEE_{tot}.

[c] Changes in the minus direction mirrored changes in the positive direction for all variables in the table.

[d] The standard DEE_{tot} under all conditions of radiation and wind is 110.4 kJ.

[e] Costs include *BMR*.

thermoregulation, production, and activity. DEE_{tot} values could be in error if there were trends in energy expenditure throughout the activity period, but no daily trends were apparent when the data were analyzed separately in four activity periods: before 0900, 0900–1200, 1200–1700, and after 1700.

SENSITIVITY ANALYSIS

Because it was necessary to estimate many parameters in the *DEE* model, the effects on outcomes of the model were analyzed by varying each parameter by 10–25%. These sensitivity analyses were run under four conditions of radiation and wind, and at three different combinations of air and ground temperatures (Tables 1, 2). The *DEE* values produced by the model were compared to a matching standard, which had identical SW radiation and windspeed values. Because the model used to calculate *DEE* varied with environmental conditions (i.e. the metabolic rate calculated from the Aschoff and Pohl equation multiplied by 1.2 was compared to that produced by the T_e model, and the higher value was used in calculating a perching metabolic rate), some outputs were asymmetrical in the analyses (e.g. r_b and surface area at T_a = 10; T_g = 12°C). The percentage that input parameters were varied represents probable maximal errors in these values.

For nonincubating birds at T_a = 10, 25, and 30°C, the model is most sensitive to changes in the values of the cost of perching, the mass of the bird, the surface area of the bird, and the cost of flight. At T_a = 10°C, the model is also highly sensitive to changes in body resistance. Variation of other variables, to the degree indicated in Table 1, led to less than a 2% change in DEE_{tot} under all conditions specified.

Errors in the cost of perching can have a large impact on *DEE* due to the large fraction of time occupied by this activity (Ettinger and King 1980). A 25% error in the value of perching metabolic rate at T_a = 25 or 30°C leads to a 13% change in DEE_{tot} under all radiation and wind conditions, while at T_a = 10°C a similar error leads to a 21% error in DEE_{tot}. A 10% change in mass with T_a = 25 or 30°C caused a 6% increase in DEE_{tot}, while for T_a = 10°C the increases and decreases were 5%. Errors in DEE_{tot} resulting from 25% errors in surface-area approximations produced a change in $DEE_{tot} \leqq 9\%$ (Tables 1, 2). Flight occupied a small percentage of the day but was an energetically expensive behavior. A 25% change in the cost of flight caused a 5% change in DEE_{tot} at 25 and 30°C and a 4% change in DEE_{tot} at T_a = 10°C. A 25% decrease in r_b at 10°C caused an 11% increase in DEE_{tot} at high windspeeds and a 9% increase in

DEE_{tot} under low windspeeds and low radiation. r_b was utilized only when T_e's were below 14°C, and this occurred commonly only during the unmated and pre-nest-building phases (less than 7% of all other phases combined had unshaded T_e's below 14°C). Therefore, these are the only phases of the study that could be much affected by errors in r_b.

The major value of such sensitivity analyses is to indicate which variables need to be measured with the greatest accuracy under specified environmental conditions. To set confidence limits on model outputs of DEE_{tot} when all errors are combined is more difficult. The probability of all errors being simultaneously additive is scant, however (some will cancel others of opposite sign), so a probable 95% confidence limit should lie in the range of ±5% of the *DEE* predicted by the model.

RESULTS AND DISCUSSION

BASAL AND THERMOSTATIC EXPENDITURE

The percentage of the total daily energy expenditure devoted to basal and thermostatic requirements (*BMR* and *TR*, respectively) ranged from 67%, in females caring for fledglings, to 86%, in incubating females. *BMR* plus *TR* averages, seasonally, 78.1% of DEE_{tot} in males and 76.1% in females. Only 12% (range 5.5–19%) of DEE_{tot} is consumed by thermoregulation in males and 9.6% (range 5.5–15.3%) by thermoregulation in females. Approximately 99% of the thermoregulatory costs accrued at night, as daytime temperatures rarely fell below 14°C. A comparison of these data on the percentage of power consumption due to *BMR* plus *TR* with extant data shows my values to be the highest yet known. Kendeigh's range of estimates for House Sparrow (*Passer domesticus*) (67–80%) *BMR* plus *TR* comes closest to the Mockingbird values (Kendeigh 1972).

The large fraction of DEE_{tot} accounted for by basal and thermoregulatory power consumption in this model, relative to previous models, probably stems primarily from the limits of our knowledge on the energetic costs of behaviors. This model assumes that, under a given set of environmental conditions, all daytime activities in nonincubating birds, other than bipedal locomotion and flight, cost a constant amount. Previous models (e.g. Mugaas 1976, Walsberg 1978, Ettinger and King 1980) have assumed that nonflight activities (e.g. perching, singing, foraging) other than *BPM* are more costly, which decreases the fraction of DEE_{tot} due to *BMR* plus *TR*.

In general, energy devoted to maintenance was obligatory, but, when ambient temperature was below 14°C, birds could modify this expenditure through the differential utilization of microhabitats. T_a's below 14°C occurred during 26 of 40 sampling bouts involving nonmated males, in 7 out of 29 bouts with males in the pre-nest-building phase, and in 4 out of 28 bouts dealing with pre-nest-building females.

To investigate the role that microhabitat choice played in determining *TR* requirements during each of these phases, I determined the mean fraction of time spent in the shade and sun for each phase during periods when T_a was less than 14°C. A metabolic rate for each bird in the sun and in the shade for each of these hourly periods was then calculated. The lower of these two values was used to determine a minimum rate of energy expenditure, and this was compared to the actual rate of energy expenditure the bird experienced. An average value of potential energy savings was then obtained for each phase. Unmated and pre-nest-building males could have saved 119.2 and 53.7 $J \cdot day^{-1}$, respectively, by utilizing the physical environment in such a way as to minimize energy expenditure, while pre-nest-building females could have saved 1,110 $J \cdot day^{-1}$.

The ecological significance of these potential energy savings can be investigated by converting these energy equivalents into food resources. Pyracantha berries were commonly utilized on many territories during these phases and have a mean energy content of 1.24 $kJ \cdot berry^{-1}$ ($n = 2$; $\bar{x} = 18.4\ kJ \cdot g^{-1}$, $s = 0.20$). Thus, under these environmental circumstances microhabitat choice for energy savings is of little importance. Nevertheless, the insights into the within-habitat distribution of endotherms gained by breaking the climate space of Porter and Gates (1969) into compartments corresponding to regions within the thermoneutral zone and outside the thermoneutral zone are potentially great, as a similar approach (that of measuring functional-response rates for a wide variety of traits at different temperatures, identifying peak response temperatures for each trait, and searching for temperatures that maximize the number of traits whose peaks overlap) has proven to be for ectotherms (Brett 1971, Huey and Stevenson 1979).

VARIATIONS OF ACTIVITY AND *DEE* BETWEEN AND WITHIN REPRODUCTIVE PHASES

Ordering the data according to reproductive phase allows the detection of energetic correlations among reproductive, other biotic (e.g. predation and food resources), and abiotic factors. Those phases imposing the strictest limitations on time budgets and requiring the greatest mobilization of resources can thus be revealed. Using phases of the breeding cycle as standards for data collection also allows for precise comparative studies within a taxon that may reveal life-history or behavioral adaptations, allow them to be correlated with habitat changes, and suggest causes for adaptation (Lack 1968).

Unmated phase.—During this phase males spent relatively little time in flight (Table 3). Foraging was restricted to fruits available within the territories, and males generally hopped or ran from bush to bush. Aggressive displays toward robins (*Turdus migratorius*) were common. Because of the low tendency to fly, the small home range sizes, and the short active daylength (Table 4), DEE_{act} [DEE_{act} includes the costs of production and activity alone (Ettinger and King 1980)] for the males reached a seasonal low during the nonmated phase.

Pre-nest-building phase.—Birds first formed a pair bond on 10 January. Quantitative observations of this phase were made between 19 February and 26 May. Several birds moved into this phase more than once during this study. Male home-range sizes were of intermediate values, and time spent in flight slightly increased over that of unmated males, primarily due to the exploration of surrounding areas (Table 3, 5). Increasing temperatures compensated for increasing active daylength and the increased percentage of time spent in flight, so that males' DEE_{tot} remained constant between these two phases (Tables 3, 4). The females' range in energy expenditure was more tightly clustered than that of the males (4.0–4.8 kJ·h^{-1} to 3.9–6.4 kJ·h^{-1}, respectively). Females did not explore surrounding areas during this phase.

Nest-building birds.—Nest building required 2 days for the three pairs of birds observed. Nest construction began on 20 February. Time-budget observations in this phase were made on a single mated pair. The male spent more time in *BPM* during this phase than in any other phase of the study (Table 3), mostly in

TABLE 3. Mean[a] percentage of the active day spent in three activities, and mean energy allocation and expenditure (DEE_{tot}) for Mockingbirds in all phases of the study.

Phase	Minutes of data	Number of birds	Percentage of active day spent			*DEE* (kJ·day^{-1}) spent					
			Perching	*BPM*	Flight	*BMR* + *TR*	Perching[b]	BPM	Flight	Egg production	Total
Unmated	1,768	6	94.5 (94.2)[c]	2.3 (2.2)	3.2 (3.6)	85.1	6.5	0.5	8.1	—	100.2
Pre-nest-building (♂)	1,646	3	94.0 (93.3)	2.0 (2.4)	4.0 (4.3)	79.7	8.0	0.6	11.9	—	100.2
Pre-nest-building (♀)	1,422	3	94.5 (95.0)	2.8 (2.4)	2.7 (2.6)	79.9	8.1	0.8	8.1	—	96.9
Nest-building (♂)	372	1	91.3 (91.3)	4.5 (4.5)	4.2 (4.2)	80.2	6.5	1.1	10.6	—	98.4
Nest-building (♀)	347	1	93.7 (93.7)	1.8 (1.8)	4.5 (4.5)	80.3	6.7	0.4	11.2	11.2	109.8
Incubation (♂)	136	2	95.0 (93.6)	2.0 (2.5)	3.0 (3.9)	78.8	8.4	0.6	9.1	—	96.9
Incubation (♀)	1,183	3	96.1 (96.1)	1.0 (0.9)	2.9 (3.0)	64.8	1.3	0.3	8.7	—	75.1
Nestlings (♂)	1,100	3	91.7 (90.4)	1.3 (1.5)	7.0 (8.0)	75.8	8.4	0.4	22.6	—	107.2
Nestlings (♀)	1,170	3	90.9 (91.0)	2.1 (1.8)	7.0 (7.2)	75.5	8.3	0.6	22.6	—	107.0
Fledglings (♂)	1,228	2	90.6 (90.9)	1.2 (1.3)	8.2 (7.8)	77.6	8.3	0.3	26.8	—	113.0
Fledglings (♀)	759	2	89.7 (88.1)	1.1 (1.2)	9.2 (10.7)	76.4	8.0	0.3	29.2	—	113.2

[a] Values are the mean of all individual birds' means.

[b] Perching, *BPM* and flight values are for the amount of power consumption above *BMR* plus *TR*.

[c] The bracketed numbers are actual mean values; the unbracketed numbers are the means of the means.

TABLE 4. Calculation of mean DEE_{tot} for each phase of the study.

Date	Phase of cycle	Daytime expenditure ($J \cdot h^{-1}$)	Day hours available	Night-time expenditure ($J \cdot h^{-1}$)	Night hours available	DEE_{tot}
10 February	Unmated	4,422	12.0	3,930[b]	12.0	100.2
15 April	Pre-nest-building (♂)	4,594	14.6	3,532	9.4	100.2
15 April	Pre-nest-building (♀)	4,364	14.6	3,532	9.4	96.9
1 May	Nestbuilding (♂)	4,652	15.2	3,142	8.8	98.4
1 May	Nestbuilding (♀)	5,131[c]	15.2	3,610[c]	8.8	109.8
5 May	Incubation (♂)	4,381	15.3	3,434	8.7	96.9
5 May	Incubation (♀)	3,307	15.3	2,816	8.7	75.1
21 May	Nestlings (♂)	5,149	15.8	3,142	8.2	107.2
21 May	Nestlings (♀)	5,138	15.8	3,142	8.2	107.0
24 May	Fledglings (♂)	5,356	15.9	3,434	8.1	113.0
12 May[d]	Fledglings (♀)	5,538	15.6	3,284	8.4	113.2

[a] Activity begins 15 min before civil twilight in the morning and ends 15 min after civil twilight in the evening.

[b] Nighttime temperatures were as follows: 10 February, 5.5°C; 15 April, 10.0°C; 1 and 21 May, 14.4°C; 5 and 24 May, 11.1°C; 12 May, 12.8°C.

[c] Includes 468 $J \cdot h^{-1}$ production.

[d] Female data collected for this phase were centered around 12 May; male data around 24 May.

collecting twigs. He contributed 4–6 twigs per hour, compared to the female's range of 0–1 twigs per hour. Females increased power consumption substantially during this phase due to egg formation (Table 3). Except for this expense, the female's time and energy budget was essentially identical to the male's.

Incubation phase.—Incubation lasted approximately 13 days in the one nest observed in detail. Similarly, Laskey (1962) found incubation periods from 12 to 12.5 days in 18 nests. Male Mockingbirds neither incubated nor fed the female at the nest. Both male and female power consumption reached a seasonal low during the incubation phase (Table 3). Females actually flew for a slightly greater percentage of time in this phase than they did in the pre-nest-building phase, but increasing temperatures, combined with the large amount of time spent on the well-insulated nest (mean for active portion of the day = 78.2%), led to an overall decline in DEE_{tot}. This decline is in accordance with the theory of Walsberg and King (1978b) that the incubation phase is a period of reduced power consumption because of shifts within the entire time/energy budget.

Birds with nestlings.—The nestling period lasts 12 days. All nests contained two young. Average male and female time/energy budgets during this phase were virtually identical (Table 3). Males and females substantially increased the percentage of the active day spent in flight. Males devoted a greater percentage of their flight time to predator defense, however, while females generally used flight as a means to reach a broader range of foraging habitats.

The ranges in the mean values of daytime energy expenditure were large for both males and females (4.0–8.2 $kJ \cdot h^{-1}$ and 3.9–7.9 $kJ \cdot h^{-1}$, respectively). Males varied greatly in the amount of time devoted to feeding offspring and predator defense. Observations of male 1 suggest that he fed nestlings more frequently (4 times in 1 h) than did male 3 (who fed nestlings but 7 times in 18 h of observation). Male 3 spent a large amount of energy fending off potential predators. He attacked crows, (*Corvus brachyrhynchos*), American Kestrels (*Falco sparverius*), dogs, and a Northern Harrier (*Circus cyaneus*) during the observation periods. The variation in female values was caused by differences in foraging ranges. Female 2 utilized a large home range and spent a mean of 11.2% of her active day in flight, whereas female 1 spent a mean of only 3.9% of her active day in flight while utilizing a smaller home range. For females, an increase of time in flight did not reflect a greater number of feedings at the nest. Female 1 fed her young 6 times in 1 h. Female 2 fed her young in 11 of 12 h of observation, with a mean of 3.6 items (fruits or insects). Females apparently feed young at greater rates than males during the nestling phase (this study, Utter 1971).

Fledgling phase.—Only pair 1 raised an off-

TABLE 5. Home-range sizes.

Bird	Phase of cycle	Date(s)	Area (ha)
Male 1	Pre-nest-building, nest-building, nestlings	8 February–11 April	0.58
	Pre-nest-building	12 April	1.63
	Fledglings	10 May	1.66[a]
	Fledglings	26 May	1.33
Male 2	Pre-nest-building	21 April	1.96
	Nestlings	20 May–26 May	2.92
	Nestlings	27 May	5.28
	Nestlings	3 June	7.06
Male 3	Pre-nest-building	22 April	4.73
	Nestlings	22 May–26 May	7.76
	Pre-nest-building	27 May	11.00
Male 4	Unmated	18 February–19 February	0.42
Male 5	Unmated	3 February–7 February	0.11

[a] Also includes a 415-m flypath to a small grove of trees.

spring that survived. This bird left the nest on 10 May and was still being fed by the parents when the study was terminated on 16 June.

Males and females reached peaks in seasonal values of DEE_{tot} and DEE_{act} during this phase (Table 3). The relatively long active daylengths and the increase in the percentage of the active day devoted to flight combined to produce this effect (Tables 3, 4). Both males and females fed the young. The male of pair 1 fed the young very little early in the phase (1 time in 7 h). During the same time span, the female fed the two offspring a mean of 6.1 fruits or insects per period ($n = 18$). Ten days after nest departure, the male bird started constructing another nest and simultaneously slowly began to take over the feeding of the fledged offspring. By the time incubation was initiated by the female, the male had taken over the feeding of the fledgling completely, providing a mean of 6.5 fruits or insects per hour ($n = 9$).

INTERPHASIC COMPARISONS AND TRENDS

Unmated and incubating birds spent significantly less energy than birds caring for nestlings ($P < 0.05$) or birds caring for fledglings ($P < 0.01$) (t-test, Steele and Torrie 1960). Incubating birds also spent significantly less energy than pre-nest-building birds ($P < 0.05$). Pre-nest-building birds spent significantly less energy than either birds caring for nestlings ($P < 0.05$) or birds caring for fledglings ($P < 0.05$). No statistical tests were attempted on nest-building birds because of the small sample sizes. Statistical comparisons of DEE_{act} yielded similar results.

The pattern of interphasic variation in DEE_{tot} almost certainly does not reflect an ultimate pattern of time and energy expenditure evolved by these birds. More likely, it is produced by variations in a particular set of proximal factors in the birds' environments. Major proximal factors that have the potential of varying between phases are social structure (territory attainment and defense, pair-bond formation), daylength, the physical environment, the demands of eggs or young, predator pressure, and resource abundance.

Unmated males showed extreme territorial aggression in January and February when breeding territories were being obtained. Pair-bond formation did not increase energy expenditure over that of territorial defense alone (compare unmated and pre-nest-building males; Table 4), and even the additional demand of building a nest while holding a mate and a territory did not increase the amount of energy devoted to activity.

Increasing daylengths allow more young to be produced, but it is the production of young that causes the energy requirements to change, not increases in daylength. A comparison of BMR plus TR costs between phases shows that the physical environment's impact on variation between phases was small (Table 3). The energy demands of production (eggs, then maintenance and growth of young) increase as the phases progress (Ricklefs 1974). This causes the total energy demands of parents and young to

TABLE 6. Total energy expenditure (DEE_{tot}) and energy expenditure in activities above the basal and thermostatic requirements (DEE_{act}) during the time period required to raise young to a state of free existence. In the mid-fledgling phase, females begin a second brood, while males care for fledglings of the first brood.

		kJ·phase^{-1}			
		Male		Female	
Phase	Days	DEE_{tot}	DEE_{act}	DEE_{tot}	DEE_{act}
Pre-nest-building	5.5	551	113	595	155[a]
Nest-building	2.0	197	36	220	59
Incubation	12.0	1,163	217	901	124
Nestlings	12.0	1,286	377	1,284	378
Fledglings	37 ♂♂, 13 ♀♀	4,181	1,310	1,481	478
Nestling/egg formation	7.5	—	—	933	360[a]
Incubation	12.0	—	—	901	124
Nestling	4.5	—	—	482	142
Total, kJ		7,378	2,053	6,797	1,820
Mean kJ·day^{-1}		108	30	99	27

[a] In the model, egg formation occurs during the last 5.5 days of the pre-nest-building phase, so 11.2 kJ·day^{-1} have been added to values from Table 3 when appropriate.

increase throughout the season. Further energy demands are elicited by the increase in the number of potential predators, which occurred with the start of the incubation phase and extended to the fledgling period (eggs, nestlings, and fledglings are assumed to have higher probabilities of being preyed upon than adults). As adults moved into these phases their devotion of time and energy toward potential predators increased (Utter 1971, this study). Data collected show that unmated and pre-nest-building birds ocassionally attack Scrub Jays (*Aphelocoma coerulescens*), but do not attack American Crows; nest-building and incubating birds attack jays and crows but not cats or dogs; birds with nestlings display agonistic behaviors toward crows, cats, dogs, and hawks; and birds with fledglings assaulted crows, cats, and dogs during the time that their fledglings were alive. The extra energy demands imposed by predators differ from the increased demands due to development of young in that they can vary from habitat to habitat or even territory to territory.

When food abundance increases, extra energy demands do not necessarily lead to increases in energy expenditure in obtaining food. Energy expenditure did increase as the phases progressed, however, largely as a result of increases in flight time due to predators and home-range expansion (Tables 3, 6). Home-range expansion allowed birds to forage in additional areas and suggests that food supply and/or quality did not increase commensurately with energy demands.

A large percentage of time was devoted to perching during all phases. This seems to be a regular feature of avian lifestyles (Ettinger and King 1980). At least a portion of this perching time is not involved with foraging. Ettinger and King (1980) have suggested that Wilson's (1975) "principle of stringency" may account for the evolution of this portion, which they have termed the "loafing" component. In the population that I studied, and for passerines in general, this is probably not the case. It is improbable that birds would decrease their fitnesses by foraging for greater periods of time when conditions were favorable because later they might have to contend with an unpredictable event such as cold weather, rain, or snow that would reduce the food supply. Birds have, no doubt, evolved life-history traits in response to this type of environmental unpredictability, but a behavior such as time devoted to foraging should be more proximally flexible than a life-history trait (Warner 1980). Predation pressure is probably a primary selective force determining the "loafing" component. Utter (1971) found that alert perching by Mockingbird males reached a maximum during the nestling phase and was at a seasonal minimum when the birds were unmated. He too felt that this "perching" or "loafing" component was ultimately determined by predation pressure. Furthermore, predation on passerine eggs and nestlings is common in many temperate-zone species (36.2% of eggs laid are prevented from developing into adults due to predation; Ricklefs 1969), and it is a common assumption, although difficult to prove, that organisms occupied with tasks (e.g. mating, foraging) experience higher predation rates than those perched or sitting. In this study, the number of times that perched birds caught sight of predators before I did suggests that birds that devote more time to perching are better able to protect themselves, and their offspring, from predation.

Between-pair comparisons suggest that variation in territorial quality can have pronounced fitness effects. Pair number 1 were the first to form a pair bond and appeared to have the greatest resource density on their territory. They utilized smaller home ranges, they spent significantly less time in flight than other pairs in the pre-nest-building ($P < 0.05$) and nestling phases ($P < 0.05$) (the only phases where sample sizes were large enough to warrant comparisons), they appeared to make more feeding visits to the nest per unit time, and they were the only birds to raise an offspring that survived after leaving the nest.

Seasonal Summary of Parental Investment

A breeding-cycle summary indicates that males have both a larger total power consumption and a larger power consumption due to production and activity than do females (Table 6). This is caused primarily by the extended period of fledgling care, which elevated male power consumption during times when females incubated.

Parental investment may be defined as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving at the cost of the parent's ability to invest in other offspring" (Trivers 1972). Relative parental investment plays a large role in the evolution of mating systems and mating behaviors. In Mockingbirds it can be divided into five components: territorial defense, production of eggs, incubation, protection of offspring, and rates of feeding offspring. Because these components have different units (i.e. time, energy, or risk), it is difficult to distill a single quantitative value for parental investment made by males and females. Nevertheless, there are two approaches that can act as rough measures: (1) qualitative statements can be made about each component and a balance sheet drawn up, and (2) DEE_{act}, because it contains all production and activity costs, can serve as an index of parental investment.

In Mockingbirds, territorial defense is a male-biased behavior involving primarily the devotion of energy resources and risk; egg production and incubation are done totally by the female, the former requiring energy, the latter, time; the protection of offspring is skewed toward the male and demands the use of energy and involves risk; and the feeding of offspring demands the use of time and energy for prey capture and appears to be female-biased during the nestling phase but male-biased during the fledgling phase. This summary suggests that there is a qualitative balance between parents in parental investment. Males have higher DEE_{act} than females over the total breeding cycle (Table 6). Therefore, males may have a slightly greater energetic investment in offspring than females.

Taken together, these two measures indicate that there is little sexual bias in parental investment (male and female investments are both needed throughout the cycle if offspring are to be raised), and this is a major determinant of the overwhelmingly monogamous mating system of Mockingbirds.

Interpopulation Comparisons

The behavioral categories used in this study match well only the flight category in Utter's (1971) study of Mockingbirds. Mockingbirds breeding in California and New Jersey spend similar amounts of time in flight (Table 7). The mean percentage of time that male birds in California spent in flight during the whole cycle was 5.5%, whereas Utter's values for two male populations were 7.3% and 6.0%. A comparison of home-range sizes shows that birds in New Jersey had slightly larger average maximal home ranges (7.9 and 7.6 ha in New Jersey vs. 6.5 ha in California), which may account for the lower flight times of the California population.

A major difference between birds in New Jersey and California is that the changes in time spent in flight between phases do not parallel each other. New Jersey males reached a primary peak with fledglings and a secondary peak while females incubated. In California, flight means peaked with nestlings, and a much

TABLE 7. Interpopulation comparison of percentage of active day in flight.

Phase of cycle	This study[a]	Utter's study (1971) Population 1	Utter's study (1971) Population 2
Unmated	3.6	6.1	3.2
Pre-nest-building	4.3	6.5	5.3
Incubation	3.9	7.4	7.8
Nestlings	8.0	6.4	5.3
Fledglings	7.8	10.1	8.3
Mean %	5.5	7.3	6.0

[a] Utter used actual means, so I present actual means for comparison.

smaller percentage of time was devoted to flight during incubation ($\bar{x}$ = 3.9%) than was found in New Jersey (7.4 and 7.8%). Ecological causes for these differences remain obscure, as Utter gave no reasons for fluctuations in flight times between phases.

Simpson (1978) also collected data on resting, foraging, and flight for Mockingbirds in Maryland. No numerical results are presented, but time spent resting significantly increased during the fall and winter, while flight time significantly increased during the nestling phase ($P < 0.05$).

Hence, over a broad geographic range Mockingbirds expend greater amounts of energy and time being active in the nestling and fledgling phases than in other portions of the breeding cycle. If increased flight time due to nutritional demands is mandatory, then a greater degree of constraint is imposed on the time budget during these phases. Partitioning the necessary flight time nearly equivalently between the male and the female (Table 3) may be a tactic that minimizes the selective impact of this constraint on the pair.

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HARLAN'S HAWK
(*BUTEO JAMAICENSIS HARLANI*):
A VALID SUBSPECIES

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ABSTRACT.—During surveys of 19 different rivers in central and southwestern Alaska, north of the Alaska Peninsula, all Red-tailed Hawks (*Buteo jamaicensis*) seen were either *B. j. harlani* or *harlani* intergrades, demonstrating that *harlani* does have a breeding range exclusive of other Red-tailed Hawk subspecies and is, therefore, a legitimate subspecies. The range of *harlani* intergrades was widespread and overlapped the *harlani* breeding range entirely. The findings presented suggest that the breeding range for *harlani* and its intergrade forms, exclusive of other Red-tailed Hawk subspecies, is: west to Norton Sound, east to the Alaska Range west slope, north to the tree line, and south to the Alaska Peninsula. *Harlani* may have diverged morphologically from other Red-tailed Hawks by isolation in a Pleistocene epoch glacial refugium, as has been suggested for other northern bird groups. The possibility of paripatric speciation, however, must also be considered. The characteristics of red in the tail (even small amounts) and white body plumage are discussed as likely intergrade traits. *Received 22 March 1982, accepted 23 September 1982.*

OF the seven North American Red-tailed Hawk subspecies recognized by the American Ornithologists' Union (1957, 1973), *harlani* is the most strongly differentiated and, together with *alascensis* and perhaps *umbrinus*, the least well known. Extensive variation of plumage within subspecies, combined with considerable subspecific breeding-range overlap and interbreeding, complicates the application of the rules of taxonomy.

Confusion concerning the Harlan's Hawk form can be traced back as far as 1829, when no less a person than John James Audubon described as *Falco harlani* (after R. Harlan a physician and naturalist) a hawk he had shot in Louisiana and called the Black Warrior (Audubon 1830: Plate LXXXVI; 1840). Despite doubts about the eventual adult plumage of the apparently immature type specimens painted by Audubon (Taverner 1927), one type specimen in the British Museum showed the characteristic Harlan's Hawk mottled tail pattern (Hellmayr and Conover 1949). It gradually became evident that the Harlan's Hawk was a member of the genus *Buteo* and was related to the Red-tailed Hawk, but whether it should be considered a separate species or a subspecies of the Red-tailed Hawk has remained in some doubt. Another opinion was that Harlan's Hawk was simply a local color phase of the Red-tailed Hawk, which did not require a scientific name of its own. At Ridgway's (1890) suggestion, the Harlan's Hawk was regarded as a subspecies of the Red-tailed Hawk (A.O.U. 1895). Some, however, still considered Harlan's Hawk a distinct species (Peters 1931). Harlan's Hawk was again considered a species in 1957 (A.O.U. 1957) but then reassigned subspecific status in 1973 (A.O.U. 1973).

Because *harlani* interbreeds freely with neighboring subspecies, it is clearly unacceptable as a species under the biological species concept (Mayr 1969). Subspecies by definition must possess a geographic breeding range exclusive of conspecific subspecies, however, and no such range was previously found for *harlani* (Taverner 1936, Gabrielson and Lincoln 1959, Godfrey, 1966). Taverner (1927: 8) analyzed records in the Yukon Territory and northern British Columbia and concluded that "If *harlani* is not racially pure here it seems hopeless to look for racial purity in it anywhere."

This paper presents new information from the field showing that *harlani* does have a discrete breeding range exclusive of other Red-tailed Hawk subspecies, along with discussion of causes for divergence and intergrade traits.

STUDY AREA AND METHODS

Subspecific identifications were made in the field during June, July, and August 1979, 1980, and 1981

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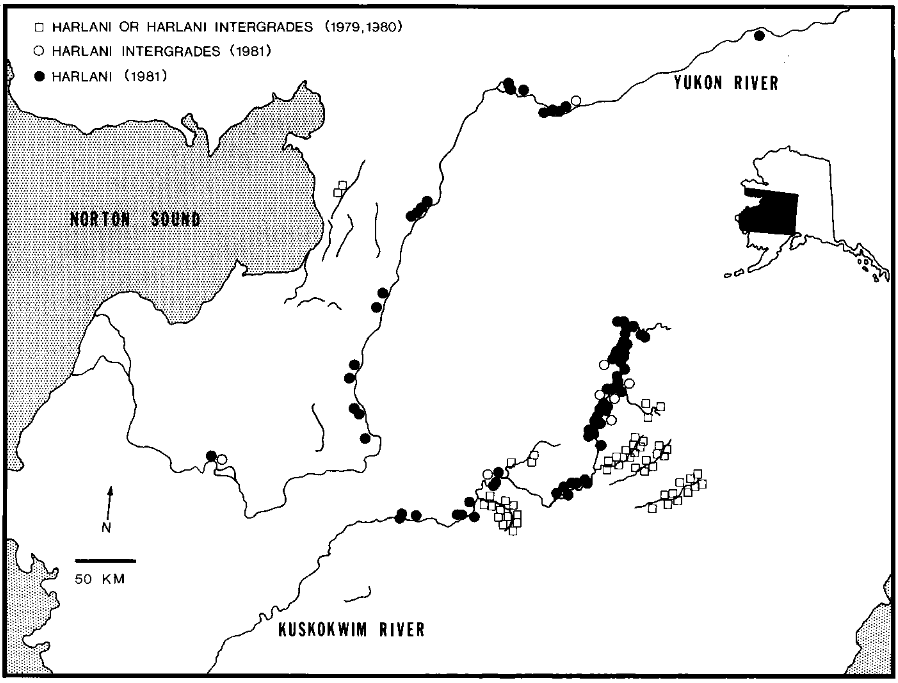

Fig. 1. Study area and distribution of Red-tailed Hawk sightings in southwestern Alaska during 1979–1981. All Red-tailed Hawks seen were either *Buteo jamaicensis harlani* or *B. j. harlani* intergrades. Distinction between these two groups was made during 1981 only. Surveys were conducted on all rivers shown.

in central and southwestern Alaska north of the Alaska Peninsula (Fig. 1). Nineteen rivers were travelled in the Kuskokwim, Yukon, and Unalakleet river drainages. Rivers in the Kuskokwim drainage included the Kuskokwim, Takotna, Tuluksak, Stony, Selatna, Tatlawiksuk, Cheeneetnuk, Gagaryah, East Fork George, and Oskawalik. Those west of or within the Yukon River drainage included the Yukon, North, South, Chiroskey, Old Woman, Golsovia, Otter Creek, Canyon Creek, and Stuyahok. All rivers were in the range of boreal forest and between 60° and 65° latitude and 154° and 162° longitude. Principal vegetation types were spruce-hardwood forest, consisting of white and black spruce (*Picea glauca*, *P. mariana*), paper birch (*Betula papyrifera*), and balsam poplar (*Populus balsamifera*), shrub thickets, and moist tundra (Viereck and Little 1972). Fuller descriptions of the survey rivers are found in Mindell (1983).

During 1979 and 1980, adult Red-tailed Hawks, which I could see well through 7 × 50 binoculars or a 20× spotting scope, were classified as either being or not being of the group *harlani* and *harlani* intergrades. No attempt was made to distinguish intergrades from "pure" *harlani*. In 1981, Red-tailed Hawks were classified as either *harlani*, *harlani* intergrades, or hawks with red-colored tails (Fig. 2). I used dorsal views of the tail in classifying Red-tailed Hawks whenever possible.

Red-tailed Hawks having tails with various combinations of white and dark-brown mottling, freckling, and streaking and with less than approximately 10% red color were counted as *harlani*. *Harlani* is characteristically dark and lacks the predominating red color in the tail that other Red-tailed Hawk subspecies have. *Harlani* frequently has a light or mottled bib; it is not consistently found, however. Light spotting on the breast, back, and wing linings is also a good field mark, when present. Hawks with tails having more than 10% red color but still having white and/or brown mottling and streaking were considered *harlani* intergrades. Hawks with tails having less than 10% red color but with extensive barring (n = 2) were also classed as intergrades. Intergrades showed wide variation in the amounts of red, mottling, and barring in the tail and in the amount of light breast color. Hawks with tails of more than 85% red color and lacking any of the distinctive *harlani* mottling were classed as hawks with red-colored tails.

Three Red-tailed Hawk subspecies, with tails predominantly red in color, have apparent zones of contact with *harlani*. *Calurus* frequently has a light colored breast, although often washed with rufous. Melanistic *calurus* individuals can be distinguished from *harlani* by their red-colored tails or lack of mottling and lack of light color in the tails. *Kriderii* could be mistaken for a light-phase *harlani* intergrade, as both may have tails with white and varying amounts

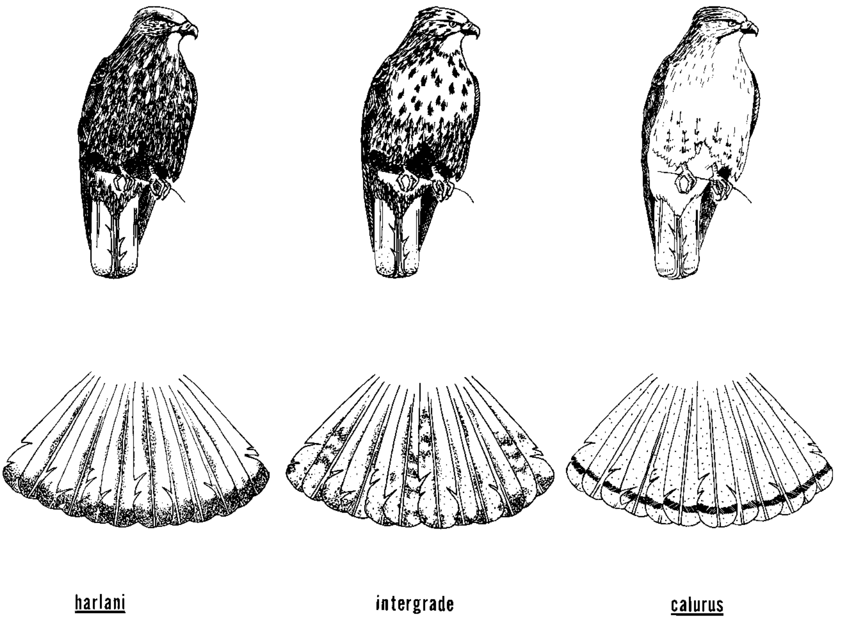

Fig. 2. Three forms of Red-tailed Hawk (*Buteo jamaicensis*) found in Alaska. The drawings are typical representations; characteristics varied widely within each of the forms, however. Widely spaced stipplings in the tails of the *calurus* (entire) and intergrade (distal half) forms denote red color.

of rufous color; however, *kriderii* are apt to be even paler than light *harlani* intergrades. *Alascensis,* although slightly smaller and darker, is virtually indistinguishable from *calurus* in the field (see Friedmann 1950 for subspecies descriptions). Red-tailed hawks in juvenile plumage were not classified to subspecies.

Results and Discussion

Subspecies and intergrade identification.—A total of 187 sightings of adult Red-tailed Hawks was made at a range close enough to allow subspecific identification in 1979–1981. All were either *harlani* or *harlani* intergrades (Fig. 1). One hawk had a tail about 70% red and 30% white with mottling, and two had tails about 60% red and 40% white with mottling. The rest had tails that were 25% or less red. The majority showed no discernable amounts of red. The Alaskan breeding range found to be exclusive to Red-tailed Hawks of the *harlani* subspecies ran from Farewell at the east slope of the Alaska range, north to Tanana and the Yukon River, west to Norton Sound, and south to St. Marys and Aniak.

I differentiated between individuals of apparently pure *harlani* and partial *harlani* (intergrades) ancestry on the basis of tail plumage in 1981, when a total of 82 Red-tailed Hawks was seen at close range on the Yukon, Kuskokwim, and Stony rivers. Of these, 73 (89%) were pure *harlani* and 9 (11%) were *harlani* intergrades. Ratios of *harlani* to intergrades were 89% to 11%, considering the Kuskokwim River alone ($n = 52$), and 90% to 10% on the Yukon River alone ($n = 19$). Field observations are an imperfect substitute for examination of preserved specimens. Specimens collected during migration or winter, however, are inappropriate for a determination of breeding range, and collected Alaskan breeding birds are few. The field identifications probably provide a conservative estimate of the frequency of occurrence of intergrades, because they were based only on tail characteristics, and some hawks with subtle intergrade characters may have been misclassified as *harlani.*

Taxonomic status and breeding range.—Because *harlani* freely interbreeds with other Red-tailed Hawk subspecies in zones of contact (Taverner 1927, Lowe 1978), it cannot be a good species. Treatment of *harlani* as a semispecies (*sensu* Amadon 1966) would assume partial reproductive isolation in contact zones with other subspecies. The evidence available does not suggest this; more data on subspecific ratios

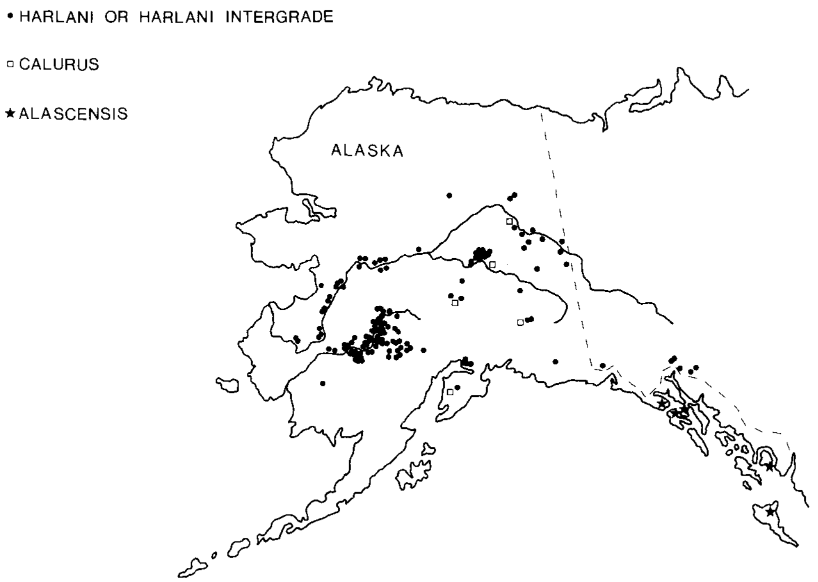

Fig. 3. Distribution of Red-tailed Hawk subspecies in Alaska and adjacent Canada. Locations for *calurus* and *alascensis* are based on specimens only. Records not from the present study are from: Grinnell (1909), Swarth (1911), Cumming (1931), Gabrielson and Lincoln (1959), Williamson et al. (1965), Kessel and Springer (1966), White and Haugh (1969), Lowe (1978), Ritchie and Curatolo (1980), and from D. Weir, C. M. White, S. Ambrose, and M. Amaral (pers. comm.).

within pairs in contact zones, however, are needed. This leaves two possibilities: *harlani* is either a distinct subspecies of the Red-tailed Hawk or a color phase of another subspecies, either *calurus* or *kriderii* (Mayr 1942: 150).

Two factors made the possibility of *harlani* being a color morph of *kriderii* initially attractive. *Harlani* and *kriderii* share the morphological character of often having large amounts of white in the tail, a trait unique among Red-tailed Hawks. *Harlani* and *kriderii* overlap in the location of core wintering areas on the Great Plains of the south-central United States. During migration, *harlani* passes over the breeding range of *kriderii* in southern west-central Canada and adjacent portions of the United States, and overlaps the general migratory route of *kriderii* as well. *Calurus* has a strongly marked melanistic phase and can resemble *harlani*; *calurus*, however, retains the red tail color.

Despite similarities, however, *harlani* does not qualify as a polymorph variant of either *kriderii* or *calurus*. Polymorphism is an intrapopulation phenomenon, and the genes involved in polymorphism have, in general, conspicuous discontinuous effects (Mayr 1970: 90). Thus, if *kriderii* and *harlani* were different morphs of the same subspecies, one would expect to see both varieties in mixed occurrence through most of their range. Overlap in breeding range has been recorded (Taverner 1936, Gabrielson and Lincoln 1959), although to only a minor degree. The Alaskan *harlani* breeding population and the *kriderii* population of the north-central U.S. and southern prairie-provinces of Canada remain distinct, with little mixing (see Friedmann 1950 for general *kriderii* range). The same can be said of *calurus* and *harlani*, although their zone of breeding range contact is broader than that for *harlani* and *kriderii*. As distinct populations with different geographic core areas, *harlani*, *kriderii*, and *calurus* are good subspecies. The similarities between *harlani* and *kriderii* suggest a close historical affinity.

The fact that all individuals seen in central and southwestern Alaska were either *harlani* or *harlani* intergrades clearly indicates the existence of a breeding range for *harlani* in which other Red-tailed Hawk subspecies do not occur (Fig. 3). Subspecies by definition must possess an exclusive geographic breeding range, and, thus, the field observations from Alaska provide the information that has previously been lacking to support subspecific status for *harlani* (cf. Mayr and Short 1970: 38, 89).

The presence of intergrades within the breeding range of a subspecies does not invalidate the exclusiveness of the range. Interbreeding can be expected to occur where two subspecies come into contact, and intergrade forms will often penetrate farther into the opposing parental ranges than will pure forms (Mayr 1942, 1963). The zone of intergradation for *harlani* entirely overlaps its breeding range within the study area (Fig. 1) and, I suspect, in the remainder of its range as well. Intergrades in the study area occured at a southwestern extreme of Pilot Village, east to the McGrath vicinity, and north to Galena. Intergrades outside the study area are recorded from Fairbanks (Lowe 1978), Atlin, British Columbia, and two southwestern Yukon Territory locations (Taverner 1927). *Harlani* remains a meaningful subspecies, regardless of the wide intergradation zone, due to its recognizability in migration and on wintering grounds and the usefulness of this trait in studying geographic variation in the species. Even individuals of partial *harlani* ancestry can often be recognized as such.

Harlani makes the longest migration of any Red-tailed Hawk subspecies and passes over (leapfrogs) some populations of other subspecies. This further illustrates *harlani*'s uniqueness and weakens any consideration of it as a color morph of another subspecies. Differences in length, duration, and chronology of migration for different subspecies influence differences in physiological timing of breeding cycles. Vaurie (1961a) and White (1968) point out the importance of migratory habits in showing a taxon's nomenclatural distinctiveness.

The exclusive breeding range of *harlani* is not strictly limited to the present study area, although it appears to include the core. Reports of Red-tailed Hawks identified to subspecies in Alaska and adjacent Canada are few, and sometimes unreliable. Twitchell's reports of *calurus* from the Innoko, Nushagak, lower Kuskokwim, and Iditarod rivers (Gabrielson and Lincoln 1959) around 1917 are not included in Fig. 3. These locations are in or near the present study area and conflict with recent observations. The reports make no mention of *harlani* intergrades, and it seems possible that Red-tailed Hawks with red-colored tails seen by him had some less visible *harlani* tail characteristics.

Five specimens identified by Gabrielson and Lincoln (1959) indicate that *harlani*'s zone of contact in central and eastern Alaska is with *calurus,* which is generally the predominant subspecies throughout most of western North America (Friedmann 1950, Brown and Amadon 1968). *Alascensis,* a smaller and richly pigmented subspecies of southeast Alaska and coastal British Columbia (Grinnell 1909, Cumming 1931), probably contacts both *harlani* and *calurus* inland. *Borealis,* with the core of its range in eastern North America, has poorly known western range limits and no demonstrated contact zone with breeding *harlani.* Todd's (1950) *B. j. abieticola* may replace *borealis* in the spruce-fir belt of Canada, although it is infrequently recognized. *Kriderii,* generally of the central North American plains, may contact *harlani,* although the evidence is small, based on possible intergrades discussed by Taverner (1927) and a juvenile specimen from Eagle, Alaska identified by Robert Ridgway (Bailey 1916).

The summer and breeding records of *calurus* closest to the eastern limit of the present study area are from the Chatenika River and Minto Lakes west of Fairbanks, the Kasilof River and Tustumena Lake on Kenai Peninsula (Gabrielson and Lincoln 1959), and in the vicinity of Ferry along the Fairbanks Highway (Kessel and Springer 1966). Some of these sightings may have been of *harlani* intergrades. Specimens identified as *calurus* by Gabrielson and Lincoln (1959) came from Salcha Slough (50 km southeast of Fairbanks), Chitina River (a Copper River tributary in south central Alaska), Denali National Park, and Circle. Additional *calurus* reports are from the Chandalar River, Robertson River, Circle, Gulkana, and Chitina River (Gabrielson and Lincoln 1959).

In the only detailed previous study of Red-tailed Hawks in Alaska, Lowe (1978) reports that, of 285 Red-tailed Hawk sightings within a 300-mi^2 study area in the Fairbanks vicinity, 83.9% were pure *harlani.* Although Lowe classified the remainder as either *calurus, borealis,* or unknown, he reveals the mixed character of most of them in stating (1978: 32), "Most of the hawks classified as *borealis* or *calurus* were not typical of these forms . . . many had tails only washed with red . . . and portions being mottled, barred or white." Lowe gives a photo-graph of an adult labeled as *calurus* that clearly has intergrade characters.

In the Yukon Territory, *harlani* are apparently predominant in the southwestern portion of the province (Yukon River drainage), *harlani* intergrades and hawks with red tails are mixed on the west slope of the Ogilvie Mountains, and hawks with red tails are common northeast of the Ogilvie Mountains in the Peel and Porcupine river drainages (David Mossop pers. comm.). More fieldwork and specimens are needed throughout northwestern Canada and Alaska to fill in details of Red-tailed Hawk geographic variation.

Reports of *harlani* occur throughout central and eastern Alaska south of the Brooks Range. The northernmost record is from the Porcupine River near the Alaska-Yukon border (Ritchie and Curatolo 1980). Additional records are from the Yukon River between Circle and the Fortymile River confluence (White and Haugh 1969), the Fairbanks vicinity (Kessel and Springer 1966, Lowe 1978), Ferry and Denali National Park (Kessel and Springer 1966), Tok and Northway (D. Weir pers. comm.), the Charley River (S. Ambrose, M. Amaral, and C. M. White pers. comm.), and Kechumstuk and McCarthy (Gabrielson and Lincoln 1959). Williamson et al. (1965) report seeing only *harlani* during the breeding season at unspecific locations in the area "west of the Copper River Valley, including the Cook Inlet region." They also record nests of *harlani* near Anchorage and at Hidden Lake on the Kenai Peninsula and two specimens collected at mile 20 on the Tok Cutoff Road.

The findings suggest that the breeding range for *harlani* and its intermediate forms, exclusive of other Red-tailed Hawk subspecies, can be outlined as follows: west to Norton Sound and the western limit of the taiga approaching the Yukon-Kuskokwim Delta; east to the Alaska Range west slope; north at least to the Koyukuk River mouth and probably up to tree line south of the Brooks Range; and south to the Iliamna Lake region. Even if a few other Red-tailed Hawks are located in this area, domination of *harlani* in subspecific ratios would not be changed. Breeding sites for *harlani* found during the present study represent a westward extension in the Red-tailed Hawk's reported range (A.O.U. 1957, Brown and Amadon 1968).

Causes for divergence.—The two basic patterns of speciation resulting in geographic variants within a widespread species are allopatric and paripatric (also alloparipatric) (Endler 1977) or geographic and semigeographic (Mayr 1942, 1963). Allopatric speciation involves the isolation and subsequent divergence of a population caused by extrinsic, geographic barriers. Allopatric speciation due to glaciation and concomitant biotic refugia has been hypothesized by Hultén (1937) to explain phytogeographic patterns and the present ranges of Alaskan plants. Pleistocene glaciation as an isolating mechanism allowing speciation among northern birds has been discussed by Austin (1932), Rand (1948), Pitelka (1950), Drury (1953), Cade (1955), Fay and Cade (1959), and Selander (1965). Much supportive information on geology, oceanography, palynology, and paleontology around the Bering Land Bridge is presented by Hopkins (1967).

The morphologically distinctive *harlani* population may also have developed through isolation in a Pleistocene epoch glacial refugium. The Bering Sea-Yukon Refugium and its possible relationship with geographic variation in the Rough-legged Hawk (*Buteo lagopus*) has been discussed by Cade (1955). A similiar argument for the evolution of *harlani* in Alaska can be made. A northern population of *B. jamaicensis* might have become isolated by surrounding ice sheets in a land area encompassing southwestern Alaska, part of eastern Siberia and the interlying Bering Sea. Morphological divergence occurring during isolation developed more rapidly than did any intrinsic isolating mechanisms that might have prevented breeding with the parental stock. Thus, *harlani* was still able to breed with Red-tailed Hawks from unglaciated regions in southern North America when corridors opened during the retreat of the last glaciation. Evolution of *harlani*'s migration is another matter, as present migration patterns for all species have apparently evolved since the end of the last glaciation (Moreau 1972, see Dingle 1980).

Buteo jamaicensis and *B. buteo* are considered by some to be members of the same superspecies group (Voous 1960, Mayr and Short 1970), although relationships in this group remain obscure. *Harlani* isolation in the Bering Sea-Yukon Refugium suggests the possibility of contact (gene flow) during that period with the easternmost form of *B. buteo*, *japonicus*. *Buteo buteo* has not been recorded in the Soviet Union east of the Kolyma River system, including

Kamchatka Peninsula (Vaurie 1961b); the eastern limit of *japonicus,* however, may be incompletely known.

Glaciation and paleoclimatological refugia represent only one of the two broad patterns of speciation. Although Mayr (1963) has previously argued against the likelihood of paripatric speciation, Endler (1977) presents a strong case for its feasibility and further demonstrates that it is not possible to distinguish between the result of paripatric or allopatric speciation simply by interpreting a particular geographic pattern. Under the paripatric mode of speciation, *harlani* would have developed through the formation of clines, without any barriers to gene flow occurring in the contiguous Red-tailed Hawk range. Isolation would be more by distance from similar conspecifics than by geographical, ecological, or temporal factors (Huxley 1939, Timofeef-Ressovsky 1940, Mayr 1942, Murray 1972, Endler 1973).

The wide *harlani* intergrade range may imply incomplete divergence of morphological characters, assuming the variance arose through primary intergradation and paripatric differentiation, or, if one assumes the events of secondary intergradation and allopatric speciation, the wide intergrade range may suggest that the intergrades are not "unbalanced" enough to produce a well-defined intergrade zone (see discussion of hybrid zones in Mayr 1963, Endler 1977). In other words, the intergrade characters do not cause a selective disadvantage, thus allowing breeding success and spread of intergrade forms. Just as one would expect disadvantageous genetic combinations to be selected against, one could expect that characters not disadvantageous would penetrate farther into the parent populations. The character of red in the tail may fit the latter description. This could explain the frequent occurrence of small amounts of red in the tails of adults that are otherwise "pure" *harlani* in character. Friedmann (1950) describes *harlani's* tail as having ". . . from scarcely any admixture of ochraceous to a definite cinnamoneous wash . . . ." It is questionable that pure *harlani* has any red color in the tail, and the not uncommon "cinnamoneous wash" may be an intergrade trait.

On the Yukon and Kuskokwim rivers during 1981, 3 (6.5%) of 46 *harlani* seen were light breasted, while 5 (41.6%) of 12 intergrades observed were light breasted. Light body plumage for hawks with *harlani* characteristics may also be the result of subspecific interbreeding, similar to red color in the tail. The greater percentage of light-breasted forms among intergrades than among *harlani* seen during the present study suggests this possibility. Independent segregation of such traits can also be expected and would account for the three hawks seen in 1981 with light breasts but no red in the tail. Considering the degree of color variation seen in other Red-tailed Hawk subspecies, however, the existence of light phase "pure" *harlani* seems possible. Observations on the parentage of light phase *harlani* are needed.

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The **American Ornithologists' Union** will hold its Annual Meeting in New York from **26 September to 1 October, 1983.** A formal call for papers will be mailed to members by mid-April with the deadline for submission of abstracts for papers and poster sessions of **15 June 1983.** For further information on the scientific program, contact **Dr. George Barrowclough, Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024.**

Fellows and Elective Members are reminded that **nominations for Elective Members or Fellows** may be submitted to the Secretary on the prescribed form up until five months prior to the opening of the next dated meeting. The deadline for 1983 is **26 April.** Nominations for Vice President and three Elective Councillors may be made in writing to the Secretary at any time prior to the annual meeting.

The American Ornithologists' Union invites applications by **1 March 1983** for the following competitive research awards:

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Herbert and Betty Carnes Awards are intended to promote excellence in the scientific study of birds by permitting individuals an opportunity to expand the design of field or laboratory work and to explore new methods of data analysis. Applications are judged on the basis of scientific merit, importance, and originality. One or two awards of $1,000–$2,000 are made.

Students, amateurs, and others with limited or no access to major granting agencies are encouraged to apply for the Van Tyne or Wetmore Awards, while the Carnes Award is open to all individuals. Application forms and further information on the **Van Tyne and Wetmore Awards** may be obtained from **Dr. Erica Dunn, 30 Davidson Road, Aurora, Ontario L4G 2B1 Canada;** applications for the **Carnes Award** should be addressed to **Dr. Ellen D. Ketterson, Department of Biology, University of Indiana, Bloomington, Indiana 47405 USA.**

Bird Observatory. Ralph Widrig, Steven Gellman, Barbara Swarth, Susan Peaslee, Erica Buhrman, Donna Vaiano, Paul Neal, Sharon Goldwasser, Dennis Parker, John Harris, David Shuford, Stuart Johnson, John and Ricky Warriner, Stephanie Zeiler, Elliot Burch, Brett Engstrom, Leslie Smith, Bernadette Allen, Greg Caillet, Tom Pogson, Tom Cassidy, Geoff Geupel, Doug Burgess, Judy Wagner, Kim Sullivan, Janet Kjelmyr, and Tad Theimer helped with the field work and Philip Henderson, Carolyn Frederiksen, and Frances Bidstrup provided valuable observations. John and Ricky Warriner generously shared with us their knowledge of Snowy Plovers at Monterey Bay, and Charles Simis provided weather data. Jan Simis allowed us to camp on her land and extended to us very warm hospitality while we were there. David Ainley, Peter Connors, David DeSante, Marshall Howe, Harriet Huber, Frank Pitelka, and Chris Ribic provided helpful comments on the manuscript. We thank these organizations and people for their generosity. This is Contribution No. 189 of Point Reyes Bird Observatory.

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The American Ornithologists' Union offers several **Marcia Brady Tucker Travel Awards** to help defray expenses of outstanding students wishing to present research papers at the society's Centennial Meeting in New York (26 September to 1 October, 1983). To apply, send the following materials to **Douglas Mock, Department of Zoology, University of Oklahoma, Norman, Oklahoma 73019 by 1 May 1983:** (i) expanded abstract of the paper (max. 3 pp, typed, double-spaced; to include methods, major results, and scientific significance), (ii) curriculum vita, (iii) your anticipated budget of expenses, and (iv) a letter of support from the academic advisor supervising your research (which should be mailed by itself). Please note that you must provide **seven** (7) copies of everything, including the letter of support, because each application is reviewed by the AOU Student Awards Committee's seven members. Also, be advised that applying for a MBT Travel Award does not guarantee a place on the Scientific Program—each student must make arrangements for that as per the instructions given with the Call for Papers announcement.

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Published by The American Ornithologists' Union and The Oklahoma Biological Survey, the cost of each inventory is $25.00, including surface mail postage. For air mail, add $5.00 (U.S.), $5.50 (Canada, Alaska, Hawaii), $9.00 (Mexico, Central America), $15.50 (Europe, South America), or $22.00 (Asia, Australia, New Zealand, Africa). Make check or money order, in American dollars, payable to **University of Oklahoma.** Order from **Dr. Gary D. Schnell, Oklahoma Biological Survey, Sutton Hall, University of Oklahoma, Norman, Oklahoma 73019, U.S.A.**

The **First Conference on Birds Wintering in the Mediterranean Region** will be held on 23–25 February 1984 at Aulla, Italy. Emphasis will be on the ecology, ethology, distribution, and migration of birds wintering in this region. For further information and preregistration materials contact **Dr. Almo Farina, Museum of Natural History of Lunigiana, Fortezza della Brunella, 54011 Aulla, Italy.**

The **Raptor Management Information System** (RMIS) is a collection of published and unpublished papers, reports, and other works on raptor management and human impacts on raptors and their habitats. It currently consists of nearly 2,500 original papers, 160 keyworded notecard decks comprised of 15,000 key paragraphs from the original papers, and a computer program to retrieve partially annotated bibliographies by species, by keyword, or by any combination of keywords and/or species. A geographical index is under development, and new papers are added as they are received. Originally designed to facilitate land-use planning and decisionmaking by government agencies and industry, the RMIS has since grown into a powerful research and environmental assessment tool for scholars, students, consultants, as well as land managers and their staff biologists. For more information write **Dr. Richard R. Olendorff, U.S. Bureau of Land Management, 2800 Cottage Way, Sacramento, California 95825 U.S.A.**, or phone commercial (916) 484-4701 or through the Federal Telephone System 468-4701.

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IMPORTANT NOTICE TO AUTHORS

Effective with this issue (January 1983), *The Auk* will adhere to use of the common and scientific names of North American birds as listed in the Thirty-fourth Supplement to the American Ornithologists' Union Check-List of North American Birds (1982 Auk 99(3): 1CC–16CC). Please use this nomenclature when preparing manuscripts for submission to *The Auk*. Exceptions should be justified in writing to the Editor.

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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 for projects in 1983 should be submitted not later than 15 February; prospective applicants and advisors should note there will shortly be a change in the Chapman meeting and deadline schedule.** 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.**

Chapman grants during 1982, totalling $40,453 with a mean of $499, were awarded to: Jonathan L. Atwood, Speciation in the Black-tailed Gnatcatcher (*Polioptila melanura*) complex; James C. Bednarz, Cooperative polyandry in the Harris' Hawk; Craig W. Benkman, Food availability, foraging efficiency, and the regulation of crossbills (*Loxia*) in eastern North America; Thomas K. Bicak, Food resources and foraging behavior of Long-billed Curlews (*Numenius americanus*) in western Idaho; David Edward Blockstein, Reproductive behavior and parental investment in the Mourning Dove, *Zenaida macroura*; Sharon Ann Brady, Effect of habitat size on the breeding and wintering ecology of the Ovenbird (*Seiurus aurocapillus*); Gregory S. Butcher, Sexual differences in the color and behavior of the Northern Oriole; William J. Carmen, Juvenile dispersal, flocking behavior, and habitat use in the California Scrub Jay (*Aphelocoma coerulescens californica*); John H. Carothers, Foraging efficiencies in a nectar-feeding guild of Hawaiian honeycreepers at a common food source; Ralph V. Cartar, Incubation behavior of the White-rumped Sandpiper (*Calidris fuscicollis*); Michael D. Carter, Social organization and parasitic habits of breeding Bronzed Cowbirds (*Molothrus aeneus*); Christine Copenhaver, Experimental analysis of decision making in hummingbirds: the effect of resource distribution on territory defense; Robert L. Curry, Evolution and ecology of communal breeding in Galápagos Mockingbirds; William James Davis, Significance of vocalizations in the Belted Kingfisher (*Megaceryle alcyon*); Carlos A. Delannoy, Breeding biology and ecology of the Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*); Kim Craig Derrickson, Analysis of the Mockingbird (*Mimus polyglottos*) vocal repertoire for behavioral and situational correlates and seasonal trends; David F. DeSante, Stability and dynamics of a subalpine breeding bird community; Robert Jack Dowsett, Conservation plan for the relict evergreen forests of Malawi and investigation of bird populations therein; Paul J. DuBowy, Optimal foraging, resource partitioning, and community structure of western North American Anatini; Patrick J. Dugan, Investigation of the information-center hypothesis in tree-nesting herons; Bonita C. Eliason, Mating system, parental care, and individual reproductive strategies in the Blackpoll Warbler, *Dendroica striata*; Keith William Emmerson, Bird community of the laurel forest of Tenerife (Canary Islands); Robert C. Fleischer, Host choice by individual female Brown-headed Cowbirds; Frank B. Gill and Douglas Wechsler, Evolution of avian mating systems: breeding biology of a promiscuous tropical flycatcher, *Mionectes oleagina*; Steven M. Goodman, Avifaunal survey of the central Egyptian eastern desert; Kathleen Diane Groschupf, Song repertoires and singing behavior of Rufous-winged and Cassin's sparrows: functional significance of diverse singing strategies in *Aimophila* sparrows; Lise A. Hanners, Development of social behavior in Laughing Gull (*Larus atricilla*) chicks; Linda Heald, Behavioral plasticity in a Tyrannid flycatcher: effects of environmen-

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methods, and his argument is little more than an opinion. On the basis of present understanding, we conclude that piciform monophyly remains the preferred hypothesis.

ACKNOWLEDGMENTS

We thank Kenneth C. Parkes and D. Scott Wood, Carnegie Museum of Natural History, for providing specimens used in dissection. Parkes, Wood, and Mary C. McKitrick provided helpful criticisms of the manuscript. Our research is supported by N.S.F. grants DEB-8010898 (R.J.R.) and DEB-7921492 (J.C.).

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Phillips, Examination of specimens at the American Museum of Natural History; Nina Pierpont, Foraging behavior, competition, and relative abundance of woodcreepers (Dendrocolaptidae) at an Amazonian forest site; Melinda Pruett-Jones, Vocal copying in Macgregor's Bowerbird (*Amblyornis macgregoriae*); Stephen Pruett-Jones, Ecology and evolution of social organization in *Parotia lawesii*, Lawes' Six-wired Bird of Paradise; Mark D. Reynolds, Mobbing behavior of nesting Black-billed Magpies; Mark F. Riegner, Foraging ecology of the Yellow-crowned Night Heron; Emily Francesca Rissman, Hormones and social behavior in the Spotted Sandpiper, *Actitis macularia;* Gary Ritchison, Singing behavior of the Cardinal, *Cardinalis cardinalis*, with emphasis on the function of singing by females; Nicholas L. Rodenhouse, Individual and regional variability in the foraging behavior of forest passerines; Stephen R. Sabo, Mixed-species flocks of Hawaiian honeycreepers; Bette J. Schardien, Behavioral ecology of a southern population of Killdeer; Debra H. Schlenoff, The "startle" response of wild-caught birds to artificial prey; Helmut Sick, Study of specimens in the American Museum of Natural History and identification of birds from Brazil; Thomas Allen Stevens, Food hoarding by Great Grey and Lesser Grey Shrikes, *Lanius excubior* and *L. minor*, a quantitative and experimental study; Stuart D. Strahl, Ecological correlates of the social system and foraging behavior of the hoatzin (*Opiathocomus hoazin*) in Venezuela; Scott B. Terrill, Potential effects of food abundance and social environment on migratory distance in Dark-eyed Juncos (*Junco hyemalis hyemalis*); Kimberly Titus, Nest-site habitat selection patterns of woodland hawks in three temperate forest regions; Jill M. Trainer, Song dialects, communication, and social organization in Chestnut-headed Oropendolas (*Zarhynchus wagleri*) and Yellow-rumped Caciques (*Cacicus cela*); Peter B. Turchin, Determination of paternity in a polyandrous bird, *Jacana spinosa;* Katherine A. Voss-Roberts, Parental attentiveness and embryonic tolerance of thermal stress in Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*); Thomas C. Will, Behavioral ecology of species replacement: Blue-winged and Golden-winged warblers in Michigan; Pamela L. Williams, Comparison of colonial and non-colonial nesting by northern orioles in central coastal California; Kathy A. Winnett-Murray, Behavioral ecology of four Central American wrens; Barbara L. Woods, Mate-guarding and female reproductive synchrony in Barn and Cliff swallows; David A. Yokel, Mating system of the Brown-headed Cowbird in two different environments; Robert M. Zink, Allozymic correlates of dominance behavior in Dark-eyed Juncos: a reappraisal.

Correction to 1981 list: MarthLeah Chaiken received a grant for research on the functions and development of variability in some calls of the European Starling (*Sturnus vulgaris*).

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The **American Ornithologists' Union** will hold its Annual Meeting in New York from **26 September to 1 October, 1983.** A formal call for papers will be mailed to members by mid-April with the deadline for submission of abstracts for papers and poster sessions of **15 June 1983.** For further information on the scientific program, contact **Dr. George Barrowclough, Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024.**

Fellows and Elective Members are reminded that **nominations for Elective Members or Fellows** may be submitted to the Secretary on the prescribed form up until five months prior to the opening of the next dated meeting. The deadline for 1983 is **26 April.** Nominations for Vice President and three Elective Councillors may be made in writing to the Secretary at any time prior to the annual meeting.

The American Ornithologists' Union invites applications by **1 March 1983** for the following competitive research awards:

Josselyn Van Tyne Memorial Fund supports projects in any area of ornithology, with awards of a few hundred to a thousand dollars each. Successful applications usually focus on one or a few carefully defined, incisive questions, rather than on general biology or management.

Alexander Wetmore Memorial Fund supports projects involving systematics and/or the taxonomy of birds and, secondarily, studies of neotropical birds. Awards are of a few hundred to a thousand dollars. Successful applications are usually built around a well-focused, interesting question.

Herbert and Betty Carnes Awards are intended to promote excellence in the scientific study of birds by permitting individuals an opportunity to expand the design of field or laboratory work and to explore new methods of data analysis. Applications are judged on the basis of scientific merit, importance, and originality. One or two awards of $1,000–$2,000 are made.

Students, amateurs, and others with limited or no access to major granting agencies are encouraged to apply for the Van Tyne or Wetmore Awards, while the Carnes Award is open to all individuals. Application forms and further information on the **Van Tyne and Wetmore Awards** may be obtained from **Dr. Erica Dunn, 30 Davidson Road, Aurora, Ontario L4G 2B1 Canada;** applications for the **Carnes Award** should be addressed to **Dr. Ellen D. Ketterson, Department of Biology, University of Indiana, Bloomington, Indiana 47405 USA.**