B., J. J. Reyes R., Wilfrido Contreras D.) of Dirección General de la Fauna Silvestre, Secretaría de Agricultura y Recursos Hidráulicos (México, D.F.). Officials of the Mérida office of División Hidrométrica, SARH, kindly gave us access to weather data. George and Janet Cobb, Joann Andrews, and Edward Kurjack were generous hosts in Yucatán. We thank Anne Clark, Paul Mason, and two anonymous reviewers for useful criticisms of a draft of this paper. Partial support for this study was provided by The Explorers Club and by the Texas Memorial Museum-The University of Texas at Austin. The Museum of Zoology of Louisiana State University provided computer time.

LITERATURE CITED

CLARK, A. B., & D. S. WILSON. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. Quart. Rev. Biol. 56: 253-277.

CONOVER, W. J. 1980. Practical non-parametric statistics. New York, John Wiley & Sons.

KOENIG, W. D. 1982. Ecological and social factors affecting hatchability of eggs. Auk 99: 526-536.

LACK, D. 1947. The significance of clutch size. Ibis 89: 302-352.

MARTIN, M. W., & R. F. MARTIN. 1985. Nestling feeding schedules of Turquoise-browed Motmots in Yucatán, Mexico. Wilson Bull. 97: 372-374.

OREJUELA, J. E. 1977. Comparative biology of Turquoise-browed and Blue-crowned motmots in the Yucatan Peninsula, Mexico. Living Bird 16: 193-208.

SCHREIBER, R. W., & E. A. SCHREIBER. 1983. The world according to El Niño. Abstr., 101st stated meeting of Amer. Ornithol. Union, New York.

SCOTT, P. E. 1984. Reproduction of the Turquoise-browed Motmot in Yucatán, Mexico. Unpublished M.A. thesis, Austin, Univ. Texas.

———, & R. F. MARTIN. 1983. Reproduction of the Turquoise-browed Motmot at archaeological ruins in Yucatán. Biotropica 15: 8-14.

The **Frank M. Chapman Memorial Fund** gives grants in aid of ornithological research and also postdoctoral fellowships. While there is no restriction on who may apply, the Committee particularly welcomes and favors applications from graduate students; projects in game management and the medical sciences are seldom funded. **Applications are reviewed once a year and should be submitted no later than 15 January—with all supporting material.** Application forms may be obtained from the **Frank M. Chapman Memorial Fund Committee, % Jane Connelly, The American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192.**

Dr. Mary McKitrick was appointed Chapman Fellow for the period May 1985 through May 1986. She is studying the significance of individual variation in M. flexor cruris lateralis in the Tyrannidae.

Dr. Nina Pierpont was appointed Chapman Fellow for the period October 1985 through October 1986. She is studying the evolution of diversity in woodcreepers (Aves: Dendrocolaptidae).

Chapman grants during 1985, totalling $25,482 with a mean of $499.65, were awarded to: David J. Anderson, booby breeding and feeding and marine resources in the Galapagos; John Anderson, tests of cooperative foraging in the White Pelican; Dr. Bonnie Bowen, genetic structure and paternity in communally breeding jays; Angelo Capparella, effects of riverine barriers on gene flow in Amazonian forest undergrowth birds; William J. Carmen, social behavior and ecology of the California Scrub Jay; Richard Casey, the effect of social interaction during the critical period of song learning in White-crowned Sparrows; Peng Chai, avian feeding behavior and its implications for the evolution of neotropical butterfly mimicry; Jack Clinton-Eitniear, *Cathartes burrovianus*: movement patterns and systematics; Nonie Coulthard, the White-throated Bee-eater (*Merops albicollis*): a study of cooperative breeding in relation to ecological factors; Marilyn England, breeding biology of the Northern Harrier on Long Island, New York; Christian Erard, systematics of African Muscicapidae; Mark A. Finke, male parental care and the evolution of reproductive effort: an experimental test; Dr. Jon Fjeldsa, museum work for a field guide and biogeographic analysis of the Andean avifauna; Ronald C. Gaines, nest site tenacity and philopatry of the Ferruginous Hawk; Steven M. Goodman, museum tour for the birds of Egypt and project; Frederick P. Greene, determinants of guild structure among insectivorous birds; Jeffrey G. Groth, systematics of the Red Crossbill in western North America, using vocal, morphological and electrophoretic data; John M. Hagan, colonial nesting in Ospreys; Dionyssia Hatzilacos, breeding and feeding biology of the White Pelican (*Pelecanus onocrotalus*) nesting at Lake Mikra Prespa—measures for protection; P. Hibbard, John P. Dunning, Laurie M. McKean, and Richard Bowers, the efficiency of foraging behavior: an experimental approach; Geoffrey E. Hill, the reproductive consequences of sub-adult plumage

(*continued on p. 22*)

MOONLIGHT AVOIDANCE BEHAVIOR IN LEACH'S STORM-PETRELS AS A DEFENSE AGAINST SLATY-BACKED GULLS

YUTAKA WATANUKI

Institute of Applied Zoology, Faculty of Agriculture, Hokkaido University,
Kitaku kita 9 nishi 9, Sapporo 060, Japan

ABSTRACT.—Diurnal activity patterns of Leach's Storm-Petrels (*Oceanodroma leucorhoa*) and Slaty-backed Gulls (*Larus schistisagus*) were investigated. The petrels reduced activity in moonlight in May and June when the predation rate by gulls was relatively high. Petrel activity levels were inversely correlated with light intensities and the corresponding risk of predation by the gull. This suggests that nocturnal activity and moonlight avoidance by the petrel in its colony are an effective defense against diurnal predators. Activity synchronization of the petrel was most marked during the full moon, further supporting the predator-avoidance hypothesis. *Received 15 October 1984, accepted 27 April 1985.*

MANX Shearwater (*Puffinus puffinus;* Harris 1966), Leach's Storm-Petrel (*Oceanodroma leucorhoa;* Harris 1974), Fork-tailed Storm-Petrel (*O. furcata;* Harris 1974, Boersma et al. 1980), and Cassin's Auklet (*Ptychoramphus aleuticus;* Thoresen 1964, Manuwal 1974) are strictly nocturnal in their colonies and are less active on moonlit nights than on dark nights. Cody (1973) discussed the nocturnal activity of alcids as a defense against diurnal predators. Gross (1935), M. P. Harris (1966), and S. W. Harris (1974) also suggested that nocturnal procellariiforms are vulnerable to diurnal predatory gulls on moonlit nights. However, the relationship between daily activities of procellariiforms and predation risk has not been studied.

I studied Leach's Storm-Petrels and Slaty-backed Gulls (*Larus schistisagus*) on Daikoku Island. Their activity patterns are described and the nocturnal behavior of the petrels in the colony is discussed as predator avoidance.

STUDY AREA AND METHODS

The colony.—The study was conducted on Daikoku Island (42°52'N, 144°52'E), Akkeshi, Hokkaido, between late April and early October 1982. The island is 6.1 km in circumference and treeless, with the exception of birch (*Betula ermanii*) groves in the ravines. Leach's Storm-Petrel (the only petrel breeding on the island) nests in the interior parts of the island, which is covered with *Artemisa montana* and *Urtica platyphilla*. Abe et al. (1972) estimated that there were 1,070,000 breeding pairs of petrels, but a more recent estimate is 415,000 (Watanuki 1985b). About 3,500 pairs of Slaty-backed Gulls nested on maritime slopes, which are covered with *Calamagrostis langsdorffii*, isolated rock stacks, and cliff ledges. A few pairs of Black-tailed Gulls (*L. crassirostris*) nested on these sites.

The Slaty-backed Gull is an important predator of adult petrels on the island. Although Jungle Crows (*Corvus macrorhynchos*) excavated petrel burrows and ate adults, eggs, and chicks, predation by the small crow population (13 pairs) was not significant.

Activity patterns.—Observations of flying birds were made from a blind set on top of a headland about 25 m above sea level. For 5 min every 30 min, I counted all birds passing an imaginary 20 × 30-m plane oriented vertically with reference to the cliff face opposite the headland. Two 6-volt electric lights, one set horizontally and the other about 45° upward at the blind, lit the plane facing toward the sea from the lower corner to the opposite side. This reduced the effect of the light on landing birds approaching from the sea. If all the landing petrels were attracted instantaneously to the lights, the number of petrels flying through the lights would increase during the observations. However, the number was rather constant during 5-min observations (Fig. 1). A few petrels and gulls flew circularly in the lights; these were excluded from the data. Observations on moonlit nights showed that Slaty-backed Gulls did not avoid the lights. No differential response to the lights by gulls and petrels was assumed. Observations started in daylight and lasted 24 h ($n = 19$ days). Data taken during a day with dense fog (13-14 May) were excluded from the analysis because of low visibility. Data of 27-28 April were included in those of May.

Light intensity was measured by a lux-meter (±10%) set horizontally and was divided into four classes: dark (0 lux), moonlight with no cloud cover (<1 lux), twilight (1-5 × 10^4 lux), and daylight (>5 × 10^4 lux). Time of sunrise, sunset, moonrise, and moonset were from the astronomical tables for Kushiro, about 40 km west of Daikoku Island.

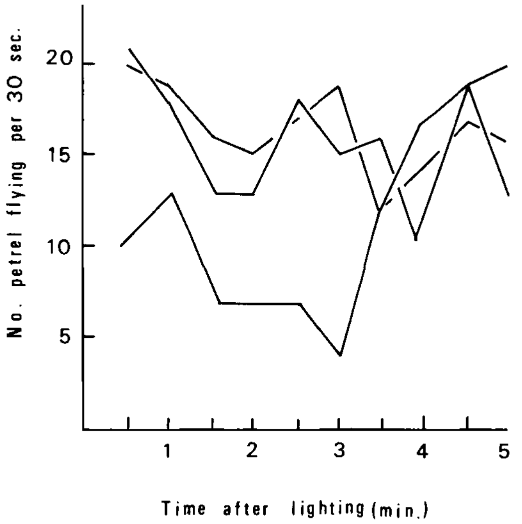

Fig. 1. Number of flying Leach's Storm-Petrels per 30 s in relation to time after lighting by two 6-volt lights, one set horizontally and the other about 45° upward. The 5-min experiment was repeated three times.

Overlap of petrel and gull activity was assessed by Pianka's overlap index (Pianka 1973):

$$O_{xy} = \Sigma\, x_i y_i / (\Sigma\, x_i^2\, \Sigma\, y_i^2)^{1/2},$$

where x_i = the number of petrels flying per 5 min and y_i = the number of gulls flying per 5 min. The time dispersion of petrel activity between 1930 and 0230 was determined by Morishita's Iδ index (Morishita 1959):

$$I\delta = K[\Sigma\, x_i(x_i - 1)] / \Sigma\, x_i(\Sigma\, x_i - 1),$$

where x_i = the number of petrels flying per 5 min and K = the number of samplings (K = 15 in this case).

Predation by gulls.—I estimated the number of Leach's Storm-Petrels eaten by Slaty-backed Gulls from the energy requirements of gulls and their food composition. The food habits of the gulls were determined by collecting pellets and food remains at their nesting sites. During the study, collections were made every 5 days in 4 study quadrats with a total of 114 nests, yielding 1,143 samples. The energy requirements of Slaty-backed Gulls were estimated by using a simple modification of the model of Furness (1978). Calculations of energy requirements and food composition of the gulls are shown in Appendices 1 and 2. The number of petrels killed was calculated for 5-day periods and was combined monthly.

Petrel breeding.—Ten 4 × 10-m study quadrats containing a total of 351 active petrel burrows were used. I checked the nests every 5 days and recorded the contents. Twenty-five pairs incubating eggs were marked by individually numbered rings. Their nests were checked every day between 4 and 9 July to determine the length of incubation stints. I estimated chick feeding frequency by weighing 15 chicks at 0900 and 2100 on 9 August, and at 0300 and 1500 on 10 August. A feeding was assumed to have occurred when a chick gained weight during this interval. This is a minimum estimate since more than one feeding may occur in the interval. Night nest attendance in the prelaying period was estimated by checking if toothpicks placed at the entrance of the active burrows the previous day were moved.

TABLE 1. Breeding schedule of the petrel and its nest duties shown by egg-days and chick-days in the study plots.

	May	June	July	Aug	Sept
No. of eggs laid	0	335	16	0	0
No. of chicks hatched	0	0	199	64	0
Egg-days	0	5,785	6,305	390	0
Chick-days	0	0	1,965	7,220	6,935

The significance of the correlation coefficient (r) and the difference between values was examined by ANOVA (Sokal and Rohlf 1969).

RESULTS

Breeding of petrels.—Petrels arrived in late April and laid eggs between early June and early July. Chicks hatched between mid-July and mid-August and fledged between late September and mid-October. The incubation duty as shown by egg-days was high in June and July, and the chick feeding duty shown by chick-days was high in August and September (Table 1).

Breeding Leach's Storm-Petrels visited their nests 0.6 times/night (a total of 63 nests visited out of 105 nests checked) in the prelaying period, fed a chick at least 1.2 times/night (n = 15), and exchanged incubation duties at 2.9 days (n = 17) on the average. These figures agree with those of other observers (Gross 1935, Wilbur 1969).

Light intensity and activities.—Leach's Storm-Petrels arrived at Daikoku Island about 1 h after sunset and left 1–2 h before sunrise (Fig. 2). The mean number of flying petrels and gulls was related to light intensity (Fig. 3). Petrels were nocturnal and rarely flew in twilight or daylight on the island. More petrels flew in darkness than in moonlight in May ($F_{1,64} = 6.50$, $P < 0.05$) and June ($F_{1,42} = 7.79$, $P < 0.01$); re-

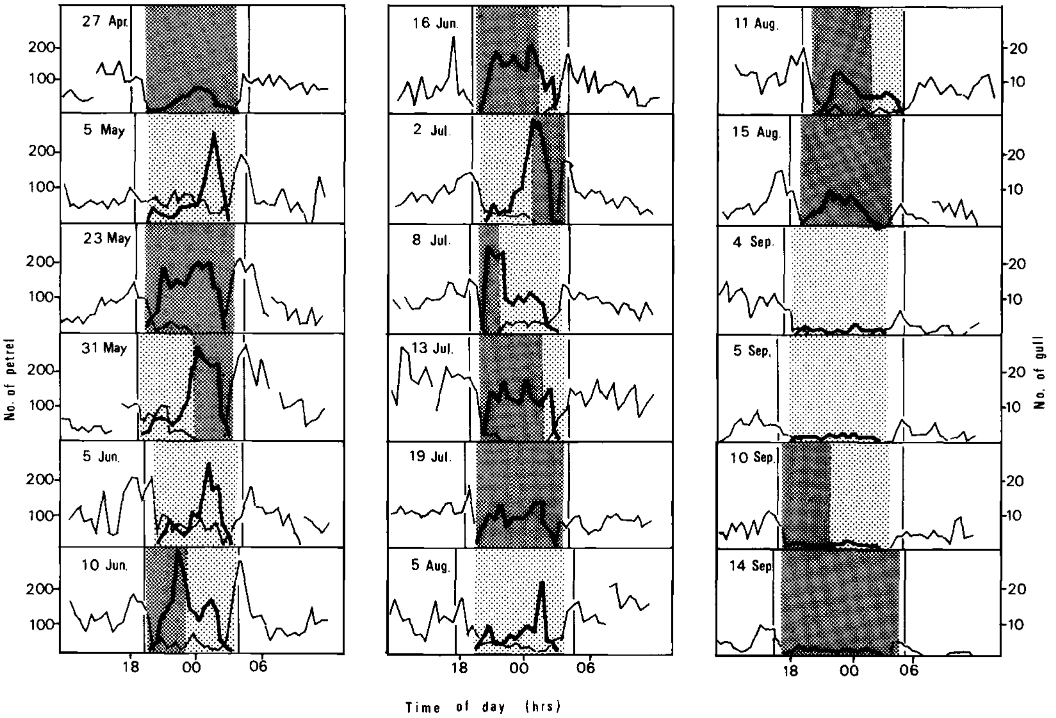

Fig. 2. Daily changes in the number of flying petrels (dark lines) and gulls (light lines) per 5 min. Heavily shaded areas represent dark times, and lightly shaded areas represent moonlight times. Vertical lines indicate sunrise and sunset.

duced activity in moonlight also occurred in July, although the difference was not significant ($F_{1,56} = 3.26$, NS). Petrels did not avoid moonlight in August ($F_{1,46} = 0.30$, NS) and September ($F_{1,72} = 3.51$, NS). The mean number of petrels flying at each light intensity was negatively correlated with that of the gulls ($r = -0.662$, $n = 20$, $F_{1,18} = 14.4$, $P < 0.01$; Fig. 3).

Slaty-backed Gulls rarely flew in the dark (Figs. 2, 3). More gulls flew in moonlight than in darkness in all the months (May: $F_{1,64} = 56.13$, $P < 0.01$; June: $F_{1,42} = 12.33$, $P < 0.01$; July: $F_{1,56} = 25.3$, $P < 0.01$; August: $F_{1,46} = 5.13$, $P < 0.05$; September: $F_{1,72} = 4.09$, $P < 0.05$). Gull activity levels were higher in twilight than in moonlight in all months (May: $F_{1,75} = 26.96$, $P < 0.01$; June: $F_{1,59} = 36.15$, $P < 0.01$; July: $F_{1,65} = 81.96$, $P < 0.01$; August: $F_{1,55} = 79.12$, $P < 0.01$; September: $F_{1,70} = 168.71$, $P < 0.01$) and higher in twilight than in daylight in May ($F_{1,123} = 34.62$, $P < 0.01$) and June ($F_{1,98} = 11.96$, $P < 0.01$).

I observed Leach's Storm-Petrels flying in daylight 11 times. Six of these petrels were killed immediately by Slaty-backed Gulls and 1 by Jungle Crows. This suggests that there is considerable potential predation risk in twilight and daylight hours.

The time overlap of petrel and gull activity, shown by ln*Oxy*, was positively correlated with the length of the period of moonlight (h; $r = 0.812$, $n = 15$, $F_{1,13} = 21.29$, $P < 0.01$; Fig. 4) when the data of the days with no overlap (i.e. $Oxy = 0$) were excluded. Encounter-rate indices (number of petrels × number of gulls) were calculated directly from Fig. 3 and were in the order moonlight > dark > twilight > daylight. I do not have direct evidence of predation under moonlight, although the indirect evidence above corroborates Gross's (1935) finding that most encounters between gulls and petrels occur during moonlight.

Activity patterns of petrels.—Most petrel activity occurred at about 2400 or between 2200 and 0100 on nights with a new moon, 0130 on nights with a full moon, 2200 on nights with a half-moon rising at midnight, and 0100 on nights with a half-moon setting at midnight (Fig. 2),

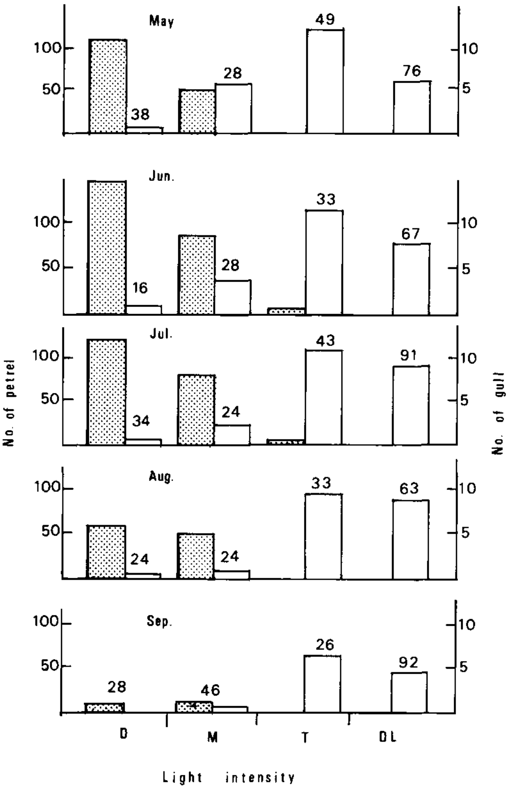

Fig. 3. Mean number of flying petrels (shaded bars) and gulls (open bars) per 5 min under dark (D), moonlight (M), twilight (T), and daylight (DL) conditions. Sample sizes of gulls and petrels are the same and are shown above the bars.

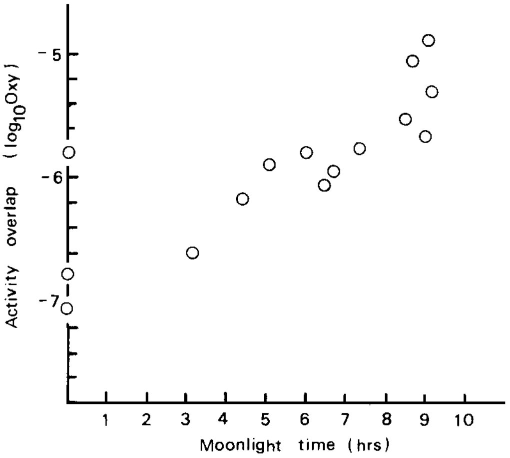

Fig. 4. The correlation between length of moonlight and activity overlap of petrels and gulls ($\log_{10}O_{xy}$).

as has been reported in Cassin's Auklet (Manuwal 1974) and in Leach's Storm-Petrel in California (Harris 1974). The petrels on Daikoku Island arrived later on full-moon nights (5–6 May, 5–6 June, and 5–6 August) and earlier on nights when the half-moon rose at midnight (10–11 June, 8–9 July, and 11–12 August) than they did on nights without a moon (27–28 April, 23–24 May, 19–20 July, and 15–16 August; Fig. 2).

On nights in May, June, and July with quarter or half-moons, the mean number of petrels flying per 5 min during darkness ($\bar{x}$ = 155.6, n = 42) was significantly higher than that ($\bar{x}$ = 100.0, n = 30) on moonless nights in the same months ($F_{1,30}$ = 37.47, $P < 0.01$). The petrels, therefore, seemed to anticipate the lunar cycle and synchronize their activity to the hours of darkness on clear nights with a half-moon, rather than reacting directly to the present light intensity. On 13–14 May, a half-moon night (moonrise at 2300) with dense fog, the peak of petrel activity occurred at 0030 rather than 2200, as would be expected if there had been no fog (the data of this day were excluded in the numerical analysis). It seems, therefore, that petrel activity is not controlled only by endogenous rhythms keyed to lunar cycles, as reported in fruit bats (Morrison 1978). Because of the low visibility on 13–14 May, petrels might have found it more difficult to locate the island and thus delayed their arrival. This suggests that petrel activity at the colony was influenced by light intensity, anticipation of the lunar cycle, and weather conditions.

On nights with a full moon, petrel activity was highly synchronized in May, June, and August but was dispersed in September (Fig. 2). The synchrony of petrel activity at night was positively correlated to the length of moonlight time in May, June, July, and August (r = 0.843, n = 14, $F_{1,12}$ = 29.47, $P < 0.01$) but not in September (Fig. 5).

Predation by gulls.—The number of flying gulls remained high in May, June, and August, but decreased in September ($F_{4,13}$ = 5.45, $P < 0.01$; Table 2) because nonbreeders and unsuccessful breeders left the colony in August and September. The total number of petrels was large in May, June, and July, decreased in August, and was small in September ($F_{4,13}$ = 8.59, $P < 0.01$;

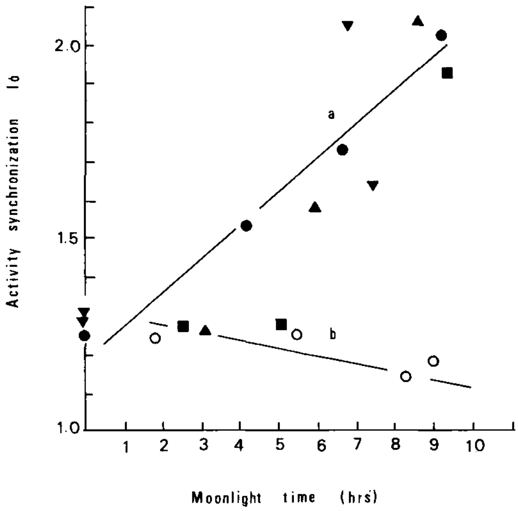

Fig. 5. The correlation between length of moonlight and synchrony of petrel activity shown by the Iδ index. ● = May, ▲ = June, ▼ = July, ■ = August, and ○ = September. Regression line a is for the data of May, June, July, and August; b is for those of September.

Table 2). The number of petrels flying at night was positively correlated with the dry-weight percentage of petrel remains (Appendix 2) in the gull diets sampled in each 5-day period ($r = 0.886$, $n = 18$, $F_{1,16} = 58.42$, $P < 0.01$).

Monthly changes in petrel numbers, numbers killed by gulls, and predation rates are shown in Table 3. Gulls ate many petrels in May and June, more in July, fewer in August, and few in September, a pattern matching the seasonal cycle of estimated gull energy requirements (Appendix 1) and food composition (Appendix 2). Thus, the monthly petrel kill appears to vary with gull energy requirements and availability of the prey.

DISCUSSION

Predator avoidance.—Slaty-backed Gulls are the most important predators of adult petrels on Daikoku Island. I estimated that annual predation by the gulls approximates 13.2% of all adult petrels. This appears to be a potentially strong selection pressure on Leach's Storm-Petrel, whose adult survival rate is high (Huntington and Burtt 1970).

The daily activity pattern of adult petrels around the colony is crucial in avoiding gull predation. Petrel adults, eggs, and chicks in the nest burrows are protected from gull predation, and petrel foraging areas do not overlap those of gulls (Pearson 1968, Wiens and Scott 1975). Therefore, only adult petrels flying on or near colonies are subject to gull predation.

The negative correlation between petrel and gull activity levels (Fig. 3) indicates that predator avoidance may be the leading cause of petrel nocturnal behavior at Daikoku. Petrels avoided moonlight in May and June when the predation rate was relatively high, but they did not avoid it in September when the predation rate was minimal (Fig. 3, Table 3). The partial correspondence between seasonal change in predation rates and seasonal variation in moonlight effects on petrel activity further supports this hypothesis.

The medium synchrony of petrel activity on nights with half-moons (Fig. 5) probably was the result of short periods of darkness in which petrels were free from predation. The greatest activity synchrony occurred on nights with the highest predation risk (full-moon nights in May, June, and August) and the least synchrony on the night without predation risk (September; Fig. 5). Numbers of flying gulls were relatively constant on the full-moon nights compared with those of petrels (Fig. 2). Therefore, highly synchronous petrel activity on these nights may dilute the predator's effects by minimizing the risk that a particular petrel encounters a gull (Wilson 1975: 41–42).

Nest duties.—Although I could not distinguish nonbreeders from breeders during observations, nonbreeders were inferred to be abundant in June and July (Ainley et al. 1974), and probably in May, because the total number of flying petrels was high in these months (Table 2). Moonlight avoidance behavior disappeared in August and September; therefore, only nonbreeders may avoid moonlight. Because nonbreeders do not have as many nest duties as breeders, the threat of predation would be a crucial factor determining their activity pattern. Eight of 12 pairs exchanged their incubation duties on a clear, moonlit night (8–9 July). This implies that moonlight does not restrict breeders' activities during the incubation period, although more data are needed to substantiate this. Harris (1966) reported moonlight avoidance behavior in nonbreeding Manx

TABLE 2. Monthly change in the mean of the total number of flying birds in 24 h.

	May	June	July	Aug	Sept
No. of days observed	4	3	4	3	4
No. of petrels ($\bar{x}$)	1,330.3	1,516.7	1,493.8	861.3	187.0
No. of gulls ($\bar{x}$)	316.5	340.7	350.5	305.7	152.3

Shearwaters, which were killed by Herring Gulls (*L. argentatus*) and Great Black-backed Gulls (*L. marinus*) (Harris 1965).

On the other hand, seasonal changes in the nest duties of breeders may contribute to the seasonal changes in the petrel response to moonlight. Breeding petrels returned to the colony more frequently in the nestling period than in the incubation period. The relative importance of nest duties in the prelaying period may be small because prelaying exodus is suggested in Leach's Storm-Petrel (Gross 1935, Watanuki 1985b). I assumed, therefore, that nest-duty activity was seasonal and correlated with the growth of chicks (Table 1). High predation risk and low nest duties seemed to cause breeders to avoid moonlight in May and June, but increasing nest duties in July might have taken priority over the high predation risk and consequently changed breeders' response to moonlight.

Bédard (1976) criticized the predator-avoidance hypothesis (Cody 1973) because there is intense predation on some alcid colonies in the Arctic, where daylight is continuous during the summer. On South Orkney Island (60°43′S, 45°38′W), where the period of darkness is short in summer, the Black-bellied Storm-Petrel (*Fregetta tropica*) is preyed on by the diurnal Great Skua (*Catharacta skua*) and shows nocturnal activity (Beck and Brown 1971). Leach's Storm-Petrels on Kent Island (44°02′N, 124°09′W) and on Little River Rock (41°02′N, 124°09′W) also are killed by diurnal gulls and show nocturnal activity (Gross 1935) as well as moonlight avoidance behavior (Harris 1974). On the other hand, Audubon's Shearwaters (*Puffinus lherminieri*) and Galapagos Storm-Petrels (*Oceanodroma tethys*) are diurnal on their breeding island, where the most important predator is a nocturnal or crepuscular owl (*Asio galapagoensis*; Harris 1969a, b). Thus, although the predator-avoidance hypothesis generally is supported, further investigations on intercolonial and interspecific variation of predation risk and diurnal activity patterns are needed.

Foraging.—Grubb (1974) suggested that abundant food in the ocean's upper waters at night has been a strong selective force toward nocturnal activity of Leach's Storm-Petrels at sea. Food of Leach's Storm-Petrels breeding on Daikoku Island may be most abundant at night (Watanuki 1985a). The petrels stay on the island for part of the night and thus lose some opportunities for feeding at night when prey is abundant. A pair exchanges incubation duties at night every 2.9 days, and hence it loses one night of feeding opportunities about every 3 days. Missed feeding opportunities seem to be potentially crucial because a petrel must recover 11% of body weight lost during an incubation stint (Watanuki 1985b). In addition, a pair feeds a chick at least 1.2 times per night and thus loses more opportunities.

Sensory constraints probably affect foraging time. If Leach's Storm-Petrels rely heavily on visual cues to locate food, they would have the advantage of feeding during the day or on a moonlit night. Leach's Storm-Petrels can locate food by smell at night as well as during the

TABLE 3. Monthly change in the number of petrels potentially available, number killed by gulls, and predation rate.

	May	June	July	Aug	Sept
No. of petrels[a]	987,700	908,700	760,500	589,300	547,800
No. killed	36,676	29,376	49,065	15,176	321
Predation rate (%)	3.7	3.2	6.5	2.6	0.1

[a] Includes nonbreeders in May, June, and July. Nonbreeders were assumed to be 16% of the total population (Wiens and Scott 1975). Unsuccessful breeders were assumed to have left the colony as soon as they failed.

day (Grubb 1972). Gordon (1955) suggested that they are nocturnal feeders, although they also feed during the day (H. Ogi pers. comm.). Direct tests of Grubb's hypothesis are lacking. Indirect evidence suggests that the petrels are not obligatory nocturnal feeders and that abundant prey at night is not always an important factor affecting the petrels' nocturnal activity at the breeding colony. In conclusion, predation risk and nest duties seem to be more important factors determining petrel activity at the colony than food availability.

ACKNOWLEDGMENTS

I thank the Akkeshi Marine Biological Station for the use of its facilities and H. Uno for his excellent logistical support in the field. H. Abe and A. C. Thoresen made valuable comments on early drafts of the manuscript, and the Board of Education of Akkeshi-cho gave permission to work on the island.

LITERATURE CITED

ABE, M., N. ICHIDA, H. SHIMIZU, M. HASHIMOTO, O. YUNOKI, N. OZAWA, & S. OZAWA. 1972. [A new attempt to estimate the number of nesting petrel, *Oceanodroma leucorhoa leucorhoa*, and wildlife of the Daikoku Island, Hokkaido.] Tori 21: 346-365.

AINLEY, D. G., S. MORRELL, & T. J. LEWIS. 1974. Pattern in the life histories of storm petrels on the Farallon Islands. Living Bird 13: 295-312.

BECK, J. R., & D. W. BROWN. 1971. The breeding biology of the Black-bellied Storm-Petrel *Fregetta tropica*. Ibis 113: 73-90.

BÉDARD, J. 1976. Coexistence, coevolution and convergent evolution in seabird communities: a comment. Ecology 57: 177-184.

BOERSMA, P. D., N. T. WHEELWRIGHT, M. K. NERINI, & E. S. WHEELWRIGHT. 1980. The breeding biology of the Fork-tailed Storm-Petrel (*Oceanodroma furcata*). Auk 97: 268-282.

BRISBIN, I. L., JR. 1968. A determination of the caloric density and major body components of large birds. Ecology 49: 792-794.

CODY, M. L. 1973. Coexistence, coevolution and convergent evolution in seabird communities. Ecology 54: 31-44.

FURNESS, R. W. 1978. Energy requirements of seabird communities: a bioenergetic model. J. Anim. Ecol. 47: 39-53.

GORDON, M. S. 1955. Summer ecology of oceanic birds off southern New England. Auk 72: 138-147.

GROSS, W. A. O. 1935. The life history cycle of Leach's Petrel (*Oceanodroma leucorhoa leucorhoa*) on outer sea islands of the Bay of Fundy. Auk 52: 328-399.

GRUBB, T. C. 1972. Smell and foraging in shearwaters and petrels. Nature 237: 404-405.

———. 1974. Olfactory navigation to the nesting burrow in Leach's Petrel (*Oceanodroma leucorhoa*). Anim. Behav. 22: 192-202.

HARRIS, M. P. 1965. The food of some *Larus* gulls. Ibis 107: 43-53.

———. 1966. Breeding biology of Manx Shearwater *Puffinus puffinus*. Ibis 108: 17-33.

———. 1969a. Food as a factor controlling the breeding of *Puffinus lherminieri*. Ibis 111: 432-456.

———. 1969b. The biology of storm petrels in the Galâpagos Islands. Proc. California Acad. Sci. 37: 95-166.

HARRIS, S. W. 1974. Status, chronology and ecology of nesting storm-petrels in northern California. Condor 76: 249-261.

HUNT, G. L., JR. 1972. Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. Ecology 53: 1051-1061.

HUNTINGTON, C. E., & E. H. BURTT, JR. 1970. Breeding age and longevity in Leach's Petrel *Oceanodroma leucorhoa*. Abstr., 15th Intern. Ornithol. Congr.: 663.

MANUWAL, D. A. 1974. The natural history of Cassin's Auklet (*Ptychoramphus aleuticus*.). Condor 76: 421-431.

MORISHITA, M. 1959. Measuring of dispersion of individual and analysis of distribution patterns. Mem. Fac. Sci., Kyushu Univ. Ser. E, Biol. 2: 215-235.

MORRISON, D. W. 1978. Lunar phobia in a neotropical fruit bat *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). Anim. Behav. 26: 852-855.

PEARSON, T. H. 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37: 521-552.

PIANKA, E. R. 1973. The structure of lizard communities. Ann. Rev. Ecol. Syst. 4: 53-74.

SIBLY, R. M., & R. H. MCCLEERY. 1983. Increase in weight of Herring Gulls while feeding. J. Anim. Ecol. 52: 35-50.

SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. San Francisco, W. H. Freeman and Co.

THORESEN, A. C. 1964. The breeding behavior of the Cassin Auklet. Condor 66: 456-476.

WATANUKI, Y. 1984. Food intake and pellet of Black-tailed Gull, *Larus crassirostris*. J. Yamashina Inst. Ornithol. 16: 168-169.

———. 1985a. Food of breeding Leach's Storm-Petrels (*Oceanodroma leucorhoa*). Auk 102: 884-886.

———. 1985b. Breeding biology of Leach's Storm-Petrels *Oceanodroma leucorhoa* on Daikoku Island, Hokkaido, Japan. J. Yamashina Inst. Ornithol. 17: 9-22.

WIENS, J. A., & J. M. SCOTT. 1975. Model estimation of energy flow in Oregon coastal seabird populations. Condor 77: 439-452.

WILBUR, H. M. 1969. The breeding biology of Leach's Storm-Petrel *Oceanodroma leucorhoa*. Auk 86: 433-442.

WILSON, E. O. 1975. Sociobiology, a new synthesis. Cambridge, Massachussetts, Belknap Press.

APPENDIX 1

Calculation of energy requirements of the Slaty-backed Gull.—A model similar to Furness's (1978) was used to estimate the energy requirement of Slaty-backed Gulls. Egg-laying, hatching, chick survival, and chick growth were monitored at 5-day intervals in the 4 study quadrats (Fig. 6). Mean daily energy requirements for egg production, chick existence, and chick growth at 5-day intervals were then estimated. The average percentage of time spent foraging away from the nest site by adults was determined by monitoring 10-20 pairs at nest sites every 30 min at night using a starlight scope. Birds away from the nests were assumed to be foraging in flight. Seasonal changes in the foraging time of breeders are shown in Fig. 6b. Percentage of flapping flight, measured by scanning flying birds for 1 min every 5 min in various wind conditions, averaged 50%. Breeders' activity requirements were estimated from foraging time, percentage of flapping flight, and energy costs of flapping and gliding flight. Foraging times of nonbreeders were not measured, but were assumed to be similar to that of breeders. Existence energy requirements of adults and chicks were estimated from their body weight and the mean daily ambient temperature.

I counted the number of adults on breeding sites and surrounding areas about every 3 weeks. About 5,000 birds were on the breeding sites in June and July. Nest-site tenacity of parents during daytime in these months was about 70%; accordingly, the number of breeders was estimated to be about 7,000. About 2,000 birds were in surrounding areas and were assumed to be nonbreeders at their maximum number in late May.

Other species-specific parameters are: egg weight at laying, 107 g ($n = 25$); adult weight, 1,100 g ($n = 1$); arrival of last breeder, 1 May; departure of first breeder, 30 July; departure of last breeder, 25 September; date of peak number of nonbreeders, 26 May. The following dates were assumed: arrival of first breeder, 1 March; arrival of first nonbreeder, 1 April; departure of last nonbreeder, 30 July. Model-specific parameters are the same as in Furness (1978).

APPENDIX 2

Food of Slaty-backed Gulls.—Pellets and food remains were dried to constant weight at about 20°C

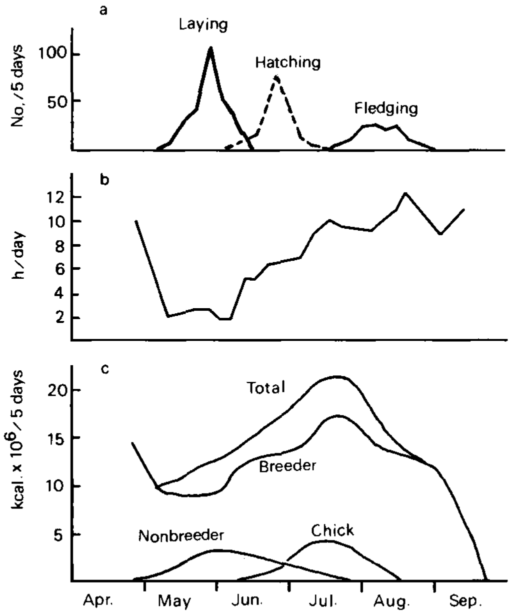

Fig. 6. Breeding phenology and energy requirements of Slaty-backed Gulls. (a) Seasonal changes in egg-laying, hatching, and fledging; (b) number of hours of foraging activity per day; (c) energy requirements. The curves in (c) represent the increasing energy requirements of nonbreeders, chicks, breeders, and the total population.

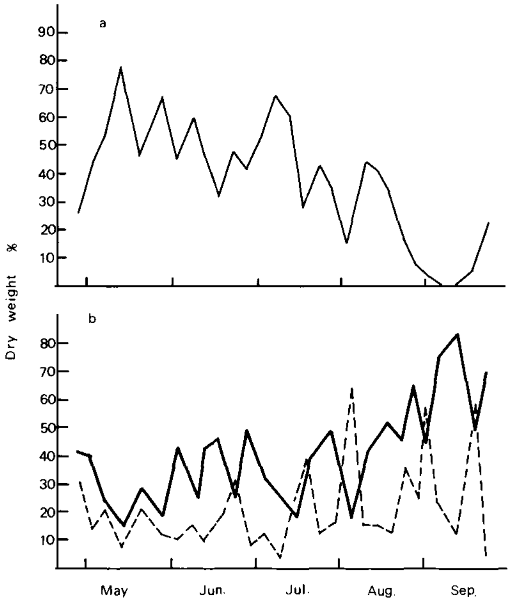

Fig. 7. Seasonal changes in diet of Slaty-backed Gulls shown by dry-weight percentages. (a) Adult Leach's Storm-Petrel; (b) fish (dark line) and other items (broken line).

for at least 30 days. Adult Leach's Storm-Petrels, fish, shellfish, crabs, and chickens were the main food items. The following equation was used to determine the total wet weight of the *i*th food: $W_i = (D_i \times R_i \times TER)/(\Sigma D_iR_iC_i)$, where D_i = dry weight of the *i*th food, R_i = regurgitation coefficient of the *i*th food (showing the ratio between wet weight of intake and dry weight of pellets), TER = total energy requirement of the gulls for 5 days, and C_i = caloric value of the *i*th food. C_is (kcal/kg wet weight) were assumed to be the following: adult Leach's Storm-Petrel, 2,600; fish, 1,500; crab with shell, 700; shellfish with shell, 500; chicken, 3,000 (Brisbin 1968, Hunt 1972, Sibly and McCleery 1983). R_is were assumed to be the same as those of Black-tailed Gulls (*Larus crassirostris*) and the following: adult Leach's Storm-Petrel, 5.9; fish, 317.3; crab, 6.7; shellfish, 2.2; chicken, 30.0 (Watanuki 1984). The number of petrels killed by gulls was calculated by dividing the total petrel wet weight by the average individual adult weight (48 g, Watanuki 1985b). Seasonal changes in the gulls' diet composition are shown in Fig. 7.

(*continued from p. 13*)

in male Black-headed Grosbeaks; Adan (Hussein) Isack, biology of the Greater Honeyguide (*Indicator indicator*); Dr. Pedro Jordano, pattern of fruit use by wintering frugivorous birds and their implications for bird-dispersed plants in Mediterranean habitats; Frank J. Joyce, nest site selection by three passerine associates of Hymenoptera; Donald M. Kent, foraging strategies of Snowy Egrets (*Egretta thula*) in the salt marshes of Massachusetts; Roni King, winter territoriality in migratory European Robins (*Erithacus rubecula*)—habitat selection and winter survivorship; Francis R. Lambert, co-adaptation between frugivorous birds and fig trees in Malaysian lowland forest; Jeanette L. Lebell, microgeographic variation in the flight whistle of the Brown-headed Cowbird; David E. Manry, a preliminary study of blood and feather pulp proteins in two South American ibis (Threskiornithidae) species; Jean-Louis Martin, the population structure of *Parus caeruleus* L. (Aves): geographical variation and speciation in the Mediterranean region; Jon Miller, breeding distribution and origin of Water Pipits in the Sierra Nevada; David Morimoto, effects of forest fragmentation on avian community structure and species-habitat relationships in the southeastern Massachusetts Pine Barrens; Jay Pitocchelli, speciation in the genus *Oporornis;* Richard O. Prum, courtship behavior and ecology of *Masius chrysopterus* in Ecuador; Dr. Michael R. W. Rands, the breeding behavior and habitat of the Arabian Bustard, *Ardeotis arabs;* Pamela C. Rasmussen, relationships of Fuego-Patagonian Blue-eyed Shags; Mark D. Reynolds, social behavior of Yellow-billed Magpies; Dr. Gary Ritchison, the significance of song repertoires in the Northern Cardinal; Jeffrey A. Schwartz, vocal similarity in mated Ring-billed Gulls as an aid in parental recognition by young; Dr. Ron Scogin, floral color and hummingbird vision; Peter E. Scott, the nesting ecology of desert hummingbirds in relation to the pollination ecology of certain nectar plants; Patricia Serrentino, the breeding ecology and behavior of the Northern Harrier (*Circus cyaneus*) in Coos County, New Hampshire; Laurie J. Stuart-Simons, food limitation in birds; Richard R. Snell, hybridization, isolation and species recognition in arctic gulls; Carol Spaw, thick-shelled eggs and their evolutionary implications; Charles Sullivan, nest behavior and development of young in the Jabiru Stork; Dr. Kimberly A. Sullivan, energetics and the development of time-budgeting; Richard John Watling, investigation of status of Ogea Flycatcher and Blue-crowned Lory; Dr. G. Causey Whittow, water loss from eggs of Great Frigatebird (*Fregata minor*); Dr. David Winkler, a general model of parental care with experimental tests on the Tree Swallow; John L. Zimmerman, *Ortstreue* in Henslow's Sparrows (*Ammodramus henslowii*) and movements in response to spring burning of tallgrass prairie.

RELATIONSHIPS AMONG TERRITORY SIZE, HABITAT, SONG, AND NESTING SUCCESS OF NORTHERN CARDINALS

RICHARD N. CONNER,[1] MARY E. ANDERSON,[2,3] AND
JAMES G. DICKSON[1]
[1]*Wildlife Habitat and Silviculture Laboratory, Southern Forest Experiment Station,*
USDA Forest Service, Nacogdoches, Texas 75962 USA, and
[2]*Department of Biology, Stephen F. Austin State University,*
Nacogdoches, Texas 75962 USA

ABSTRACT.—We collected data from 30 territories of Northern Cardinals (*Cardinalis cardinalis*) during 3 breeding seasons (1979-1981) in eastern Texas. Territory size was positively correlated with tree height and negatively correlated with the density of foliage at ground level and at 3 m above the ground, and with the density of shrubs. Nesting success was positively correlated with presence of patchy understory foliage and arthropod biomass in territories. Cardinals with low song complexity and shorter songs held better-quality territories and had better nesting success than cardinals with more complex songs. We suspect that young males may use long, complex songs to establish a territory initially, and in subsequent years put less time and effort into song and more into care and defense of young. *Received 15 January 1985, accepted 7 June 1985.*

THE functional significance of song in birds is a widely studied phenomenon. In particular, the significance of song repertoires has recently received extensive examination, resulting in many hypotheses. Krebs (1977a) summarized these hypotheses as follows: (1) repertoires enhance individual recognition (Emlen 1971, Brooks and Falls 1975); (2) repertoires are a product of sexual selection (Catchpole 1973, Kroodsma 1977); and (3) repertoires increase success in territorial competition by allowing acquisition of larger (Krebs 1977b) or better-quality (Howard 1974) territories.

Large repertoires could permit matched countersinging among males establishing or defending territories (Lemon 1968, Verner 1975) or reduce habituation of listeners (Hartshorne 1956). Krebs (1977a) suggested a new mechanism (the Beau Geste hypothesis) whereby large song repertoires could be used to create the illusion that a particular habitat area was already saturated with numerous territorial males.

Holding territory size constant, repertoire size of Northern Mockingbirds (*Mimus polyglottos*) in central and western Texas was correlated with measurements of territory quality (Howard 1974). Male mockingbirds with larger repertoires also had the highest success in excluding other males and attracting females. If males with larger repertoires or some other song characteristic are able to establish and maintain larger or better-quality territories, such males should have a higher nesting success than males with territories of lesser quality. High-quality territories should have a greater availability of food and nest concealment than low-quality territories. Females from an inbred strain of canaries (*Serinus canaria*) exposed to playbacks of males with large repertoires built nests faster and laid larger clutches than did females exposed to small repertoires (Kroodsma 1976).

Female birds may select males on the basis of song quality or select the territory of a male because of the habitat's appearance through mechanisms similar to those by which males may identify habitat quality. If either method was used, pairs in higher-quality habitat (more food and better concealment available) might be expected to produce more eggs or young on the average than pairs in lower-quality territories. Although predation would have a substantial impact on nesting success (Best 1978), vegetation structure or quality may also have an influence on predation and nesting success of birds (Best and Stauffer 1980). Vegetation characteristics around nests were correlated with nesting success of Vesper Sparrows (*Pooecetes gramineus*) in a 1-yr study in West Virginia

---

[3] Present address: Math and Science Division, Bee County College, Beeville, Texas 78102 USA.

TABLE 1. Characteristics of cardinal songs and 100 randomly selected syllables from 30 territories over a 3-yr period in eastern Texas.

Variable code	Description	Mean	SD
Songs			
ASYB	No. of syllables per song	10.45	2.49
DSYB	No. of different syllables per song	1.61	0.23
TRAN	No. of syllable transitions per song	0.62	0.23
SBVS	Total versatility of syllables per song	0.08	0.08
SLGT	Song length (s)	2.78	0.59
ISI	Intersong interval (s)	6.33	1.33
NSGS	No. of songs recorded per bird	311.27	267.87
SBRP	Syllable repertoire per male	15.50	4.52
STRP	Song-type repertoire per male	18.67	8.16
SGVS	Total versatility of song type per male	7.62	2.90
RESB	Residual of syllable repertoire	−0.22	2.76
REST	Residual of song-type repertoire	−0.16	4.26
Syllables			
FMOD	Frequency modulation (degree)	46.20	5.82
FEMP	Frequency emphasized (kHz)	2.20	0.42
HIFR	High frequency (kHz)	4.19	0.58
LOFR	Low frequency (kHz)	1.33	0.24
FRGE	Frequency range (kHz)	2.87	0.56
SYBL	Syllable length (s)	0.24	0.04
ISBI	Intersyllable interval (s)	0.13	0.02
NELM	No. of elements per syllable	2.84	1.26

(Wray and Whitmore 1979). Concealment, nest height, and adult body weight were also significantly related to nesting success in a riparian bird community in Iowa (Best and Stauffer 1980).

We examined relationships of territory size and habitat quality with song characteristics and nesting success of Northern Cardinals (*Cardinalis cardinalis*) in eastern Texas to evaluate associations of song with habitat and nesting success.

METHODS

Study area.—We selected a diverse "edge" stand (15 ha) for the study in a pine (*Pinus* spp.)-hardwood forest 15 km south of Nacogdoches, Texas. Northern Cardinals were studied in this area during three consecutive breeding seasons (1979-1981). Approximately half of the stand was mature forest (18-22 m tall); most of the remainder was a 4-yr-old loblolly pine (*Pinus taeda*) plantation with dense pine and deciduous foliage that was 2-3 m high in 1979. The mature forest and the pine plantation had patchy foliage and ranged from xeric, sandy hilltops to mesic sites along two streams. The streams ran through forested strips (30-50 m wide) in the pine plantation. Several small openings (0.45 ha total) in the mature forest had a ground cover of grasses and forbs. Dominant tree species in upland portions of the mature forest were shortleaf pine (*P. echinata*), loblolly pine, post oak (*Quercus stellata*), and sweetgum (*Liquidambar styraciflua*). Dominant tree species in the mature forest along the streams were sweetgum, American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), sweetbay (*Magnolia virginiana*), and hickory (*Carya* spp.). Winged sumac (*Rhus copallina*), smooth sumac (*R. glabra*), and sweetgum were dominant in the pine plantation.

Song recording.—We recorded songs of 30 territorial male cardinals from the end of March through the middle of June with a Uher 4000 report IC tape recorder and a 40-cm Dan Gibson Parabolic EPM P-650 electronic microphone. The time span over which we recorded songs enabled us to sample songs of all males throughout all phases of the nesting season. Males were color marked (colored bands and tarsi streamers) for individual identification. To minimize sound distortion, we made most recordings within 8-15 m of males. We did not use playbacks of song to elicit singing behavior. Only males with 89 or more songs recorded were used for analyses ($n = 30$ males).

All field recordings were reviewed at one-quarter tape speed (2.4 cm/s); syllable types (see Lemon 1965) were initially determined and identified at this reduced speed. The different syllable patterns were verified with spectrograms made on a Kay Elemetrics model 7029A Sona-Graph, using the wide band filter setting with a frequency range of 80-8,000 Hz. Information measured included the kinds and numbers of syllables in each song, song length, and intersong interval (Table 1). Song lengths and intervals were measured to the nearest 0.1 s with an electronic stopwatch.

One hundred syllables sung by each territorial male cardinal were sampled randomly and spectrograms were made of these 3,000 syllables. We made 8 measurements on each syllable: frequency range, frequency modulation, frequency emphasized, highest frequency, lowest frequency, syllable length, number of elements in each syllable, and the following intersyllable interval (after Morton 1975; Table 1). We measured the frequency emphasized at that point in the syllable where most of the energy was focused, as indicated by the darkest portion of each syllable on the spectrograms.

Frequency modulation of syllables was determined geometrically as an angular measurement of the rate of frequency change. Each syllable was divided into four equal segments, with five vertical lines; this provided five possible points of intersection with the syllable. At each point, the angle of inclination was measured in degrees with respect to the horizontal axis. Each angle was recorded as an acute angle, disregarding the quadrant in which it fell. This simplified the data by ignoring the various modes of inflection inherent in cardinal syllables. The five angle measurements were averaged and used as an index of frequency modulation, a measure of frequency change per unit of time.

The intersyllable interval was the period of silence separating the syllable measured from the syllable that followed it. This measurement was taken only between like syllables.

As measures of repertoire size, we determined the number of different syllables used by each male in all songs, as well as the number of song types used by each male (after Lemon 1965). Both the number of different syllables and the number of song types sung by each male correlated significantly with the number of songs recorded ($r = 0.69$ and 0.73, respectively; $P < 0.001$). Thus, to correct for differences in numbers of songs recorded, we calculated regression equations for each male to obtain a "predicted" number of syllables or song types for a given number of songs recorded. A log transformation of the number of songs corrected for a slightly parabolic relationship between songs recorded and both variables. We used, as new variables, the residuals for each observation (the difference between the observed number of syllables, or song types, and the predicted) that were calculated by the regression program [residual for the number of syllables (RESB): $r^2 = 0.56$, $n = 30$, $F_{1,28} = 36.2$, $P < 0.001$; residual for the number of syllable types (REST): $r^2 = 0.72$, $n = 30$, $F_{1,28} = 70.9$, $P < 0.001$; Table 1].

To evaluate song complexity, we calculated an index of syllable versatility within songs for each cardinal. Modifying a technique developed by Kroodsma and Verner (1978), total syllable-type versatility was defined as a ratio between the sources of within-song variation and the total number of syllables in a song. The formula for syllable-type versatility is written as:

$$\text{syllable-type versatility} = (a \times b)/c,$$

where a = number of different syllables/song, b = number of syllable transitions/song, and c = total number of syllables/song.

In addition to syllable-type versatility, we calculated total versatility of song types per male (SGVS) and transitions between song types as described by Kroodsma and Verner (1978) (Table 1). Song types were listed in sequence, and 10-song sequences were used to calculate total song versatility. If fewer than 11 songs were sung in a bout, total song versatility was not calculated.

Territory mapping.—We delineated the territories of Northern Cardinals by intensive spot-mapping, noting the outmost limits where each male sang (International Bird Census Comm. 1970), by observing movements of males in great detail, and sometimes by flushing males. Male and female cardinals were captured at 11 different mist-net stations (each station had a 2.1 × 12.8-m net with 3.8-cm mesh) set up throughout the study area, color marked, and released. Poor visibility and impenetrability of vegetation precluded extensive use of Wiens's (1969) flushing technique. A 40-m grid with numbered stakes and flagged poles positioned at all intersections of grid lines provided reference points for mapping territories on the entire 15-ha study area. About 230–250 h were spent from the end of March to 15 June each year (1979–1981) to determine territory boundaries. Territories were drawn on maps of the study area, cut out, and their areas measured with a LiCor conveyor belt (LI-3000) area meter.

Sampling territory vegetation.—The geometric center of each cardinal territory was located in the field by using grid maps. Three plots, 8 m in radius (0.02 ha), were centered 20 m from each territory center at compass bearings of 90°, 210°, and 330°. The height and species of trees greater than 5 cm in diameter at breast height (DBH), basal area, maximum height of vegetation, percentage of canopy closure, and foliage density were measured within these plots (Table 2).

The directions for foliage density measurements, either north and east or south and west, were determined randomly for each plot. Foliage density was estimated for ground level and for 1-, 2-, and 3-m height intervals with a 0.5-m-square (0.25 m^2) gridded board (MacArthur and MacArthur 1961). Midstory and canopy foliage density (higher than 7 m) and percentage of canopy closure above 20 m were estimated with a reflex camera (MacArthur and Horn 1969) positioned at the center of each 0.02-ha plot. Foliage height diversity (MacArthur and MacArthur 1961) and estimates of vertical and horizontal patchiness were calculated for each territory (Table 2). Vertical patchiness was calculated by subtracting foliage

TABLE 2. Habitat characteristics measured within 27 cardinal territories in eastern Texas.

Variable code	Description	Mean	SD
TF0-3	Total foliage density, ground to 3 m (m^2/m^3)	0.60	0.25
FDG	Foliage density, ground level (m^2/m^3)	0.27	0.17
FD1	Foliage density, 1 m (m^2/m^3)	0.13	0.05
FD2	Foliage density, 2 m (m^2/m^3)	0.12	0.06
FD3	Foliage density, 3 m (m^2/m^3)	0.08	0.04
FD7	Foliage density, 7-13 m (m^2/m^3)	0.04	0.06
FD13	Foliage density, 13-20 m (m^2/m^3)	0.04	0.06
FD20	Foliage density, >20 m (m^2/m^3)	0.20	0.37
%CC	Canopy closure (%)	26.85	25.36
VHGT	Vegetation height (m)	13.41	6.70
#TRSP	No. of tree species	3.12	1.97
#TRES	No. of tree stems >6 cm	7.47	3.95
TSPD	Tree species diversity (H')	0.79	0.55
BA	Basal area (m^2/ha)	8.21	5.18
#SHSP	No. of shrub species	8.37	4.92
#SHRB	No. of shrub stems	29.96	13.93
SSPD	Shrub species diversity (H')	4.24	2.16
%GC	Ground cover (%)	42.91	26.73
TSIZ	Territory size (ha)	0.64	0.14
ARBM	Arthropod biomass (g)	3.78	1.52
HPTCH	Horizontal patchiness at 2 m ($1 - J'$)	0.09	0.13
VPTCH	Vertical patchiness ($1 - J'$)	0.11	0.07
FHD	Foliage height diversity (H')	1.24	0.09

height equitability (J') from 1.0. Horizontal patchiness of shrub-level vegetation at 1, 2, and 3 m was estimated for each territory by calculating the equitability of the sums of foliage densities at each horizontal foliage sampling point and subtracting it from 1.0.

A smaller subplot (3 per territory), 1.8 m in radius (0.001 ha), was established within each 0.02-ha plot. It was randomly located 3 m from the center of the plot. The species and number of stems of all woody vegetation less than 6 cm DBH, percentage of ground cover, and average height of shrubby vegetation (vegetation <3 m high) were measured in this subplot (Table 1). Shrub species diversity (H') and equitability (J') were calculated. Percentage of ground cover was determined by looking straight down through a tube, 11 cm long and 4 cm in diameter, at the center of the subplot from 1.3 m above the ground and estimating the proportion of herbaceous cover to bare ground.

Nest observations.—While territories were being mapped and songs recorded, we searched the study area for cardinal nests. Only what we believed to be first nesting attempts were evaluated. After a nest was located, we visited it every day or two to check how many eggs or young were present. We used a mirror on the end of a pole to examine nests above eye level. Young cardinals were considered to have fledged successfully if they were seen in the nest until at least 9 days old and subsequently were not found in an undisturbed nest (Table 3). Typically, fledglings could be heard begging for food in shrubs near their nest site. Our presence may have influenced nest success (Bart and Robson 1982). The disturbance factor should have been fairly equal in all territories because all nests were visited at an equal rate, and territories in general were traversed at equivalent frequencies while mapping bird positions and recording male song. Unsuccessful nests were classified according to the most likely cause for failure: fire ant (*Solenopsis invicta*) predation or Brown-headed Cowbird (*Molothrus ater*) parasitism; undisturbed empty nest—snake or bird predator; and disturbed empty nest—mammalian predator (Best 1978).

Sampling nest-site vegetation.—An 8-m-radius plot (0.02 ha) was centered on each nest site to sample vegetation (Table 3). Foliage densities, basal area, and vegetation height were measured in the same manner as for the territory plots. At each nest, the height of the nest tree and height of the nest above ground were measured with a metric tape when possible, and otherwise with an Abney level. Estimates of nest concealment were obtained with the aid of a 0.5-m-square density board similar to the board used by MacArthur and MacArthur (1961). The board was positioned vertically 0.5 m from the nest on both a north-south and east-west bearing to estimate concealment from horizontal directions. The observer, facing the board 0.5 m from the nest on the opposite side of the nest from the board (1 m from the board), looked through the vegetation and estimated the percentage of the board that was obscured by foliage. This pro-

TABLE 3. Characteristics measured at 30 cardinal nest sites in eastern Texas.

Variable code	Description	Mean	SD
NFDG	Foliage density, ground level at nest site (m^2/m^3)	0.28	0.18
NFD1	Foliage density, 1 m at nest site (m^2/m^3)	0.23	0.16
NFD2	Foliage density, 2 m at nest site (m^2/m^3)	0.32	0.56
NFD3	Foliage density, 3 m at nest site (m^2/m^3)	0.15	0.17
NFD7	Foliage density, 7–13 m at nest site (m^2/m^3)	0.02	0.07
NFD13	Foliage density, 13–20 m at nest site (m^2/m^3)	0.02	0.04
NFD20	Foliage density, >20 m at nest site (m^2/m^3)	0.29	1.40
NVHGT	Vegetation height at nest site (m)	11.98	8.10
NBA	Basal area at nest site (m^2/ha)	7.43	5.68
NHGT	Nest height (m)	1.58	0.73
HTNT	Height of nest plant (m)	2.88	0.99
FDHZ	Horizontal foliage concealment of nest (%)	45.09	26.51
FDVT	Vertical foliage concealment of nest (%)	64.57	26.37
FLDG	No. of young fledged/nest	0.70	0.97
YONG	Maximum number of young in nest	1.04	1.15
EGGS	Maximum number of eggs in nest	2.04	0.82

cedure was repeated with the board 0.5 m above the nest and the observer 0.5 m below the nest to estimate vertical concealment. We did not measure concealment above the nest separately from concealment below the nest.

Arthropod sampling.—A crude estimate of food availability was obtained by sampling each territory with 38-cm-diameter insect sweep nets. Although not a direct sample of cardinal food, we assumed that our measure of arthropod biomass would give a relative index of the overall food availability. Five 200-sweep samples (1,000 sweeps/territory) were taken from random places on 5 different days immediately following nesting in each territory. These samples were oven dried for 48 h and weighed on an analytical balance.

Data analyses.—Of 43 territories located and studied, only 21 had measurements for all variables (≥ 89 songs recorded and all nest data). Correlation analyses were used to examine degrees of association between variables. We realize that there are potential problems associated with interpretations of multiple bivariate correlations if conclusions are focused on individual correlations. We have evaluated patterns of numerous significant correlations in this paper to gain insight into ecological relationships. Although many significant correlations were detected, we present only those relevant to relationships among territory size, habitat, song, and nesting success of Northern Cardinals. Sample sizes for evaluating degrees of relationship varied: nesting success vs. song variables, $n = 21$; nesting success vs. territory size, arthropod biomass, and vegetation variables, $n = 23$; and song vs. territory size, arthropod biomass, and vegetation variables, $n = 30$. Discriminant function analysis (Hull and Nie 1981) comparing territories that fledged young vs. those not fledging young ($n = 21$), was used to evaluate variables that might be important to nesting success. Rao's V was used as the stepwise selection method, with an F value of 3.2 set for entry of variables into the analysis. Because of unequal group sample sizes, we checked the influence of heteroscedasticity by making a log transformation on all variables and recalculating the discriminant function (DFA). The results of the DFA using log-transformed variables were consistent with the DFA using raw data, indicating the acceptability of the initial DFA (Pimentel 1979).

RESULTS

Cardinal territory size was related to vegetation structure. Territory size was positively correlated with vegetation height and negatively correlated with total foliage density from the ground up to 3 m, foliage density at ground level, and number of shrubs (Table 4). Thus, territories were larger in areas having mature trees and smaller where only shrubby vegetation was present. Previous studies have indicated that cardinals have a strong affinity for understory foliage (Dow 1970, Conner et al. 1983) and often nest in shrubs (Stauffer and Best 1980). Because understory foliage was negatively correlated with overstory foliage (percentage of canopy closure was negatively correlated, $P < 0.001$, with understory foliage variables: FDG, $r = -0.69$; FD1, $r = -0.58$; FD2, $r = -0.58$; and TF0-3, $r = -0.76$), the increase in cardinal territory size in areas where mature trees were present was not surprising. Cardinals may require a threshold amount of under-

TABLE 4. Correlations of habitat, song, territory size and quality, and nesting success of Northern Cardinals (see Tables 1-3 for variable codes). Sample size varies for the entries in this table; see Methods. Correlations with $P > 0.10$ and variables without any significant correlations are omitted from the table.[a]

	TSIZ	ARBM	SBVS	ASYB	SGVS	RESB	YONG[b]	FLDG[b]
TSIZ					0.25[c]			
ARBM			−0.34*	−0.40*			0.45*	0.40*
SBVS		−0.34*			0.32*		−0.36[c]	
SGVS	0.25[c]		0.32*					
SLGT		−0.45**		0.83***				
%GC		0.72***		−0.42*				
FDG	−0.43**	0.57***					0.43*	0.40*
FD1		0.64***		−0.34*			0.37*	0.37*
FD2						0.41*		0.51**
FD3	−0.46**		−0.30[c]		−0.36*			
TF0-3	−0.45**	0.51**			−0.29[c]	0.33*	0.38*	0.45*
FD20								
SSPD		0.54***	−0.53***			0.32*		
#SHRB	−0.37*							
HPTCH								0.41*
VHGT	0.40**	−0.33*			0.33*		−0.30[c]	−0.28[c]
#TRES		−0.44**					−0.38*	−0.46*
BA		−0.53***					−0.39*	−0.44*

[a] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.
[b] Spearman rank correlations.
[c] $P < 0.10$.

story foliage in their territories. If shrub foliage is sparse, territory size may be increased to compensate.

Arthropod biomass was positively correlated with foliage density at ground level and at 1 m, total foliage density at 0-3 m, percentage of ground cover, and shrub species diversity (Table 4). Arthropod biomass was negatively correlated with number of trees, basal area, and vegetation height.

Total syllable versatility (SBVS), our measure of within-song complexity, was negatively correlated with arthropod biomass, foliage density at 3 m, and shrub species diversity (Table 4). The average number of syllables used in each song and song length also correlated negatively with arthropod biomass. These results suggest that cardinals having the shortest and least versatile songs were on the best-quality territories. Total song versatility correlated positively with total syllable versatility but was not correlated with arthropod biomass. No other song variable was significantly correlated with arthropod biomass ($P > 0.05$).

Of our measures of repertoire size, only the residual of the number of syllables sung by males (RESB) was positively correlated with foliage density at 2 m, total foliage density from the ground to 3 m, and shrub species diversity (Table 4). This suggests an association between large syllable repertoires and vegetation characteristic of good-quality territories. Although understory foliage variables and shrub species diversity were correlated with arthropod biomass, the residual of the number of syllables was not. The residual of the number of syllables also was not significantly correlated with any measure of nesting success.

Nesting success in the long run should be the best index to what *might* be quality habitat. Although our study was only 3 years in length, some relationships were observed. Fledging success and number of young in nests were positively correlated with arthropod biomass (Table 4). The number of eggs in nests was not correlated with arthropod biomass or any other variable measured. We had originally expected clutch size to be related to food availability. Fledging success and the number of young in nests were also positively correlated with foliage density at the ground, at 1 m above the ground, and with total foliage density at 0-3 m. In addition, fledging success was positively correlated with foliage density at 2 m and horizontal patchiness at 2 m above the ground. Both fledging success and the number of young in nests were negatively correlated with the number of trees and tree basal area (Table 4).

Collectively, these results suggest that the better-quality territories were areas with fewer trees and more understory foliage. Originally, we had expected some aspect of nesting success to be positively correlated with territory size, but none was.

No significant correlation between fledging success and nest height existed ($r_s = 0.01$, $P > 0.05$). However, territories with successful nests had higher foliage density and patchiness at 2 m throughout the territory than did territories with unsuccessful nests (ANOVA, $P < 0.05$). This suggests that abundance and distribution of foliage at 2 m above the ground throughout the territory may be important for cardinals. This is reinforced by the fact that cardinal nests in the study averaged 1.6 m above the ground.

Nesting success variables were not significantly correlated with cardinal song characteristics ($P > 0.05$). However, total syllable versatility had a nearly significant negative correlation with number of young in nests ($r_s = -0.36$, $P < 0.053$). Studies conducted over a longer period of time with a larger sample are probably needed to demonstrate strong relationships between song characteristics and nesting success.

Cowbird parasitism and predation affected nesting success. Causes of nesting failures in our study area over 3 years were: 7 to Brown-headed Cowbird parasitism, 5 to small mammals and snakes, 1 to a large mammal, and 1 to fire ants. We observed partial clutch losses on 9 occasions, which may have caused an absence of correlation between the number of eggs and the number fledged ($r_s = 0.08$, $P > 0.05$). The number of young and the number fledged were significantly correlated (Spearman rank correlation, $r_s = 0.70$, $P < 0.001$). Also, nests found in early stages of the nesting cycle (nest building and egg-laying) may have had a higher probability of parasitism than nests found during the nestling phase (Mayfield 1961). Although we expected nest concealment to have an effect on nest parasitism and predation, no significant correlations existed between fledging success and foliage density in the nest vicinity (NFD1 through NFD3, Table 3) or nest concealment (FDHZ and FDVT).

A stepwise 2-group DFA using song and territory variables (Tables 1, 2) successfully discriminated between territories having successful nests (nests fledging at least one young) and territories having unsuccessful nests ($P < 0.006$, 90.5% of cases correctly classified, eigenvalue of the discriminant function = 1.048). Three variables entered the stepwise DFA: foliage density at 2 m, song length, and versatility of syllables per song. Examination of the correlations of the original territory and song variables with the discriminant axis (canonical variate) indicated that successful nests were positively associated with increasing values of foliage density at 2 m, horizontal patchiness at 2 m, vertical patchiness, total foliage density from the ground to 3 m, foliage density at 1 m (i.e. dense, patchy understory foliage), and arthropod biomass (Table 5). Successful nests were negatively associated with increasing song length, foliage height diversity, number of syllables per song, number of tree stems, and vegetation height. Thus, unsuccessful nests were associated with increasing vegetation height, density of trees, and foliage height diversity, and male territorial cardinals that sang long songs with higher within-song versatility. Results of the DFA agree closely with our interpretation of the correlation patterns among the univariate variables (Table 4).

TABLE 5. Correlations of original territory and song variables with the discriminant function (canonical variate) resulting from a 2-group DFA used to discriminate between territories successfully fledging young ($n = 7$) and territories where nests failed ($n = 14$). (See Tables 1-3 for variable codes and units.)

Variable	Pearson correlation[a]
FD2	0.75***
HPTCH	0.64***
SLGT	−0.60**
VPTCH	0.57**
TF0-3	0.54**
FHD	−0.53**
FD1	0.51**
ARBM	0.47**
ASYB	−0.46*
#TRES	−0.43*
VHGT	−0.41*

[a] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

DISCUSSION

Our results suggest some interesting relationships. Cardinals with less versatile or complex songs may hold better-quality territories (territories with more understory foliage and

TABLE 6. Song characteristics of a male cardinal that held the same territory for three successive breeding seasons (see Table 1 for variable codes and units).

Year	NSGS	SBVS	ASYB	DSYB	TRAN	SLGT	SBRP
1979	316	0.094	7.1	1.4	0.36	1.96	18
1980	398	0.140	7.5	1.5	0.50	2.41	17
1981	187	0.177	11.6	1.8	0.78	2.49	18

greater arthropod biomass) and fledge more young than cardinals with more complex songs. This suggests that natural selection would favor males with the least song complexity, a concept that at first appears counterintuitive.

Several alternative explanations may clarify this apparent contradiction. Fledging success may be confounded by factors other than overall territory quality. Predation and nest parasitism can both greatly affect nesting success and yet not be related to territory quality from a "food" perspective. Our visits to nests may have increased the probability of cowbird parasitism and predation. Although nest concealment should be related to cowbird parasitism and predation, our measurements of concealment may have been insufficient to document this relationship. Wray and Whitmore (1979) made more extensive measurements of nest concealment than we did and detected a significant relationship between foliage proximal to the nest and nesting success.

Our measures of song complexity and repertoire size may also be confounded. Howard (1974) speculated that both repertoire size and reproductive success might be correlated with age. A study of the Great Tit (*Parus major*) demonstrated that males with intermediate-size repertoires have the highest lifetime reproductive success (McGregor et al. 1981). Older male White-crowned Sparrows (*Zonotrichia leucophrys*) hold larger territories and are more often successful in breeding than young males (Ralph and Pearson 1971). Male Field Sparrows (*Spizella pusilla*) with larger territories mate more frequently than males with smaller territories (Best 1977).

Young male cardinals may use longer, highly complex songs when first establishing a territory. In subsequent breeding seasons, age or prior ownership of a particular territory may permit the male to put "less effort" into song (complexity) and allow more effort for nest defense and care of young. This hypothesis meshes with our results of song complexity being negatively related to fledging success. However, this hypothesis also suggests that song complexity should decrease over successive years. Such was not the case with one male cardinal that nested in the same territory for 3 consecutive years. Total syllable versatility, number of syllables per song, number of different syllables used per song, and song length increased steadily for this individual during the study (Table 6). Syllable repertoire (SBRP) for this male remained relatively constant, and no trend or pattern was observed with other song variables. Similarly, repertoires of Great Tits also do not increase yearly (Krebs et al. 1978). The change we observed in song complexity over time for one male cardinal is obviously insufficient to establish any trends. Studies on additional males are needed to provide sufficient data for a more accurate determination.

ACKNOWLEDGMENTS

We thank L. B. Best, D. E. Kroodsma, R. E. Lemon, C. J. Ralph, and J. Verner for numerous helpful comments and suggestions on the manuscript. This study was endorsed and funded in part by the U.S. Man and the Biosphere Program (MAB-3), which contributes to grazing land management objectives. We also thank the John Cason family and the Southland Division of St. Regis Paper Co. for use of their lands during the study. Mention of commercial products in this paper does not constitute endorsement by the USDA to the exclusion of other products that might be suitable.

LITERATURE CITED

BART, J., & D. S. ROBSON. 1982. Estimating survivorship when the subjects are visited periodically. Ecology 63: 1078-1090.

BEST, L. B. 1977. Territory quality and mating success in the Field Sparrow (*Spizella pusilla*). Condor 79: 192-204.

———. 1978. Field Sparrow reproductive success and nesting ecology. Auk 95: 9-22.

———, & D. F. STAUFFER. 1980. Factors affecting nesting success in riparian bird communities. Condor 82: 149-158.

BROOKS, R. J., & J. B. FALLS. 1975. Individual recognition by song in White-throated Sparrows. II. Features of song used in individual recognition. Can. J. Zool. 53: 1749-1761.

CATCHPOLE, C. K. 1973. The functions of advertising song in the Sedge Warbler (*Acrocephalus schoenobaenus*) and the Reed Warbler (*A. scirpaceus*). Behaviour 46: 300-320.

CONNER, R. N., J. G. DICKSON, B. A. LOCKE, & C. A. SEGELQUIST. 1983. Vegetation characteristics important to common songbirds in east Texas. Wilson Bull. 95: 349-361.

DOW, D. D. 1970. Distribution and dispersal of the cardinal, *Richmondena cardinalis*, in relation to vegetational cover and river systems. Amer. Midl. Natur. 84: 198-207.

EMLEN, S. T. 1971. The role of song in individual recognition in the Indigo Bunting. Z. Tierpsychol. 28: 241-246.

HARTSHORNE, C. 1956. The monotony-threshold in singing birds. Auk 72: 176-192.

HOWARD, R. D. 1974. The influence of sexual selection and interspecific competition in mockingbird song (*Mimus polyglottos*). Evolution 28: 428-438.

HULL, C. H., & N. H. NIE. 1981. SPSS update 7-9. New York, McGraw-Hill.

INTERNATIONAL BIRD CENSUS COMMITTEE. 1970. An international standard for a mapping method in bird census work. Audubon Field Notes 24: 722-726.

KREBS, J. R. 1977a. The significance of song repertoires: the Beau Geste hypothesis. Anim. Behav. 25: 475-478.

———. 1977b. Song and territory in the Great Tit. Pp. 47-62 *in* Evolutionary ecology (B. Stonehouse and C. M. Perrins, Eds.). London, Macmillan.

———, R. ASHCROFT, & M. I. WEBBER. 1978. Song repertoires and territory defence in the Great Tit. Nature 271: 539-542.

KROODSMA, D. E. 1976. Reproductive development in a female songbird: differential stimulation by quality of male song. Science 192: 574-575.

———. 1977. Correlates of song organization among North American wrens. Amer. Natur. 111: 995-1008.

———, & J. VERNER. 1978. Complex singing behaviors among *Cistothorus* wrens. Auk 95: 703-716.

LEMON, R. E. 1965. The song repertoires of cardinals (*Richmondena cardinalis*) at London, Ontario. Can. J. Zool. 43: 559-569.

———. 1968. The displays and call notes of cardinals. Can. J. Zool. 46: 141-151.

MACARTHUR, R. H., & H. S. HORN. 1969. Foliage profile by vertical measurements. Ecology 50: 802-804.

———, & J. W. MACARTHUR. 1961. On bird species diversity. Ecology 42: 594-598.

MAYFIELD, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73: 255-261.

MCGREGOR, P. K., J. R. KREBS, & C. M. PERRINS. 1981. Song repertoires and lifetime reproductive success in the Great Tit (*Parus major*). Amer. Natur. 118: 149-159.

MORTON, E. S. 1975. Ecological sources of selection on avian sounds. Amer. Natur. 109: 17-34.

PIMENTEL, R. A. 1979. Morphometrics: the multivariate analysis of biological data. Dubuque, Iowa, Kendall/Hunt.

RALPH, C. J., & C. A. PEARSON. 1971. Correlation of age, size of territory, plumages, and breeding success in White-crowned Sparrows. Condor 73: 77-80.

STAUFFER, D. F., & L. B. BEST. 1980. Habitat selection by birds of riparian communities: evaluating effects of habitat alterations. J. Wildl. Mgmt. 44: 1-15.

VERNER, J. 1975. Complex song repertoire of male Long-billed Marsh Wrens in eastern Washington. Living Bird 14: 263-300.

WIENS, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithol. Monogr. No. 8.

WRAY, T., & R. C. WHITMORE. 1979. Effects of vegetation on nesting success of Vesper Sparrows. Auk 96: 802-805.

FAMILY ASSOCIATIONS IN COMMUNALLY ROOSTING BLACK VULTURES

PATRICIA PARKER RABENOLD[1]
Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27514 USA

ABSTRACT.—Observations of marked individuals in a partially marked population of Black Vultures (*Coragyps atratus*) show that immediate family members maintain close contact throughout the year. Associations between mates and between parents and offspring are primarily responsible for this. Mutual allopreening, feedings, and intercessions in fights occur almost exclusively within families. Adults known to breed within the study area (neighbors) associate more strongly than nonneighbors, although not as strongly as mates. Certain families associate preferentially with certain other families. Strength of interfamily associations is not related to distance between nest sites within the study area. I argue, therefore, that birds actively seek particular individuals as associates. Further knowledge of breeding dispersal of young of known parentage will provide clues to relatedness of highly associated neighbors. Strong associations among related individuals can help explain the use of avian communal roosts as information centers. *Received 27 April 1984, accepted 10 June 1985.*

COMMUNAL roosts and breeding colonies could serve as "information centers" to which unsuccessful foragers return and follow successful individuals to a known food source (Ward and Zahavi 1973). Explaining the apparent aid-giving of successful foragers remains a difficulty of this hypothesis. Some workers emphasize the probability of high levels of relatedness within colonies (e.g. Erwin 1978, Waltz 1982) to help explain why successful foragers might tolerate any costs of being followed. By sharing food with closely related individuals, successful foragers could increase their inclusive fitness (Hamilton 1964). If mechanisms exist that allow preferential sharing with close relatives, inclusive fitness gains could outweigh costs of sharing.

Black Vultures (*Coragyps atratus*) form large communal roosts each night throughout the year, although they nest in pairs in isolated, well-protected locations. Indirect evidence suggests that Black Vulture roosts may serve as food-finding information centers. For instance, morning roost departures are significantly clumped both in time and in direction, and these clumped departures cannot be explained by weather conditions (Rabenold 1983).

A successful forager might return to the roost to recruit particular individuals with whom to share or cooperatively defend its find. If these associations of individuals are stable over time, it should be possible to detect relative differences in the strengths of associations between different individuals in communal roosting and feeding situations. There is evidence suggesting that parent-offspring ties persist for several months past fledging in Black Vultures (Jackson 1975, McHargue 1977, this study). This behavior would help explain the use of roosts as information centers. Preferential association and preferential behavioral interactions among individuals in a population could structure the distribution of benefits accruing from shared information at communal roosts. The maintenance of family associations outside the breeding season is the subject of this paper.

To examine associations of individuals within Black Vulture communal groups, I ask specifically (1) whether mated pairs and individuals of known relatedness (parents and offspring or siblings) are seen together more often than predicted by chance; (2) whether these intrafamilial associations differ from associations of the same individuals with birds not known to be related (extrafamilial associations); (3) whether pairs nesting in an area associate more than expected by chance with other pairs nesting in the same area, and whether these neighborhood associations differ in degree from associations within families or between nonneighbors; and (4) whether strength of associations between neighbors is dependent on the distance between their nest sites.

---

[1] Present address: Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907 USA.

METHODS

Study area and population.—The study area, situated in farmlands of Chatham County in central North Carolina and covering approximately 250 km^2, is composed of 60% agricultural land and 40% woodland; it contains no towns (Reeves et al. 1970). The main farm products of this area are poultry, swine, dairy and beef cattle, and tobacco produced by many small farms. I have studied the population of Black Vultures there since autumn 1976, and I began a trapping and marking program in 1977. Birds were captured primarily in a walk-in funnel trap baited with carrion. By summer 1981, 344 Black Vultures had been marked with individually numbered vinyl wing tags (Wallace et al. 1980) legible at close range with 10× binoculars and at greater distance with a 15–60× zoom telescope.

Based on the proportion of birds marked at roosts and feeding areas and an estimated annual mortality of 12.5% (the annual mortality of breeding adults during this study), approximately 1,200 Black Vultures regularly use the area year-round. Not all of these birds roost in the study area on any given night, as there is considerable movement in and out. Seasonal estimates of the number of birds present range from 358/night during winter (mean size of winter roosting groups multiplied by mean number of active roosts/night) to 242/night in summer. The range over which these birds forage is unknown, although some movement of marked birds outside the study area suggests very large ranges for some individuals. Of the 344 marked Black Vultures, over 100 are seen regularly within the study area, 2 have been seen at a distance of 95 km (and have since returned), and 1 was seen repeatedly at a communal roost 170 km away. Daily ranges are not likely to include such long movements.

The study area contains seven roost sites used by the local population. Roosts are all in mixed conifer-hardwood forest near small creeks. Roost sites are traditional in the sense that each is regularly attended when birds are feeding nearby, and local residents report that the same sites have been occupied sporadically for many years, although no roost site is occupied every night. My observations of marked birds indicate that within a certain area individuals use a number of roosts over the course of a year, but often use a single roost for several days in a row.

Censuses of feeding and roosting groups.—Each roost was censused regularly through the course of the study. If a roost was occupied, I counted the number of Black Vultures present and identified tagged birds. Censuses were usually complete, except in summer when foliage sometimes partially obscured the roost. Measures of association, therefore, represent minimum estimates of actual associations between individuals. When scanning groups for tags, I recorded all social interactions involving at least one marked bird, including mutual allopreening, fights (initiator, if seen, type of fight, and outcome), and begging by young birds (adults to whom begging was directed and whether the young bird was ignored, rebuffed, or fed by regurgitation). I performed 318 roost censuses during the study.

Feeding groups were located by following birds out of the roost to their morning feeding sites, or by driving a prescribed circuit through the study area during midmorning while watching for groups of vultures circling or descending. At all feedings, I counted the number of Black Vultures present, identified tagged birds, and recorded social interactions involving marked birds. I performed 86 feeding censuses during this study.

Ascertaining family membership.—In North Carolina, breeding Black Vulture pairs nest in isolated locations usually deep in woods. Between 1977 and 1981 I located 14 such nest sites within the study area. At 8 of these the same adults returned each year to breed. All adults at these 8 nests were marked with patagial tags. Each pair produced 1 clutch of 2 eggs each year (although 2 early failures resulted in later relaying), and all fledged young have been tagged at each nest in every year since its discovery. In all, 46 young birds of known parentage have been tagged in the 8 families, and different-age sibs (produced by the same parents in different years) are known for all sites.

Association measures.—I used only observations of feeding or roosting groups of birds to test the significance of associations between individuals in the groups. Sightings of birds at nest sites were not included. I also excluded observations made during the early breeding months of March, April, and May, when movement of breeding adults is restricted owing to incubation and brooding duties. Only the first sighting of an individual at a particular site on any day was used. To test associations within the group of birds regularly using the area, I attempted to omit transients and irregular visitors by considering only those animals sighted on at least 10 different days. If observations of two birds did not overlap completely as a result of different marking dates or disappearance of either one, the measurement of association was limited to the period of potential overlap.

Of the 344 marked Black Vultures, 102 (50 adults, 52 young) were resighted at least 10 times (maximum number of sightings for any individual in groups = 61), and these birds are considered the core group of vultures regularly using the study area. These 102 individuals were considered by pairs in three measures: the Chi-square test of independence within pairs; the point correlation coefficient *V* (Pielou 1976); and Dice's (1945) "association index." The point correlation coefficient, an index ranging from −1 to +1, was used as a comparative measure between subclasses of the population (e.g. between related pairs and unrelated pairs) and as a means of assigning direction to results of the Chi-square test (the Chi-square

Table 1. Association of 8 mated pairs of Black Vultures outside of incubation and brooding periods.

	Number of censuses including:				Measures of association[a]	
Pair	A and B (a)	A only (b)	B only (c)	Neither A nor B	χ^2	Dice's index
1	15	13	8	158	49.93	0.588
2	20	14	13	132	42.28	0.597
3	9	3	3	57	30.42	0.750
4	10	2	4	52	30.58	0.769
5	9	1	15	140	42.51	0.529
6	10	6	3	151	66.92	0.690
7	8	6	16	104	13.52	0.421
8	15	10	5	109	47.07	0.667

[a] $P < 0.001$ for all Chi-square values. Dice's index $= 2a/(2a + b + c)$.

test is two-tailed and will not differentiate between significantly positive and significantly negative associations). Dice's index was also used to make comparisons and to validate results based on the other two measures.

Results

Associations in feeding and roosting contexts.—Individual vultures usually were resighted more often at roosts than at food for two reasons: (1) I made many more censuses at roosts than at food (318 vs. 86), and (2) roosting groups were much larger than feeding groups (means = 82 and 22). While 102 birds were resighted 10 or more times, only 53 of these had at least 10 resightings at roosts and only 11 had at least 10 resightings at feeding sites. The small feeding sample makes full comparisons of association rules between the two contexts impossible. However, 7 of the 11 birds resighted 10 or more times at food were local breeders comprising 4 mated pairs. These 4 pairs did not differ between roosting and feeding contexts; all were positively associated in both situations ($P < 0.05$, χ^2 test). If a larger subsample of the 102 is examined, using birds with as few as 2, but on average 6, feeding sightings, sufficient pairs exist to compare within-family associations at roosts (68 pairs) against those at food (37 pairs). Although feeding groups are smaller and random mixture would produce many fewer positive associations at food than at roosts, the proportion of positive associations did not differ between roosts and food for mates, parent-offspring pairs, or siblings. Pooled intrafamilial associations included 32% positive associations at food, significantly more than the random expectation of 5% (χ^2, $P < 0.01$). No age-paired category (e.g. adult-adult, adult-young, young-young) composed of known family members paired with extrafamilial birds, differed significantly from 0.05 in the proportion of positive associations at feeding sites. Because association rules among family members apparently do not differ between roosting and feeding, I pooled roosting and feeding observations for the remainder of the analysis.

Associations between mates.—Mated adults alternate nest shifts of approximately 24 h during the 55 days of incubation and brooding. I have 62 observations of an off-duty bird attending a communal roost, and in 27 visits to nests at dawn I never found more than 1 adult present. Except during March, April, and May, when they were incubating and brooding, members of the 8 mated pairs with known nest sites were seen together more often than expected by chance (Table 1, χ^2, $P < 0.001$ for all). However, none showed complete overlap, as all 16 marked adults of known nest site occasionally were seen without their mates. Of the associations of these 16 individuals with all other adults that were not family members, only 18% were positive, significantly fewer than between mates (Fig. 1). Adults clearly associate with their mates more than with other adults outside the breeding season, but they also regularly associate with some adults that are not their mates.

Associations between parents and offspring.—Among parent-offspring pairs, 23 of 36 (64%) showed positive association through the course of this study (Fig. 1). I have insufficient yearly resightings of almost all pairs to test the decline of parent-offspring associations as the young birds mature, so for this analysis I pooled all parent-offspring pairs regardless of offspring age. In general, resighting rates of young birds decreased as the birds aged so that 3- or 4-yr-old offspring are resighted less frequently than either their parents or their younger siblings. However, when in the study area, subadults occurred with their parents with the same probability as did younger sibs. Associations of the 16 breeding adults of known nest site with all young known not to be their offspring yielded only 14% positive associations. Parent-offspring associations included significantly more positive associations than did parent-nonoffspring associations. The converse re-

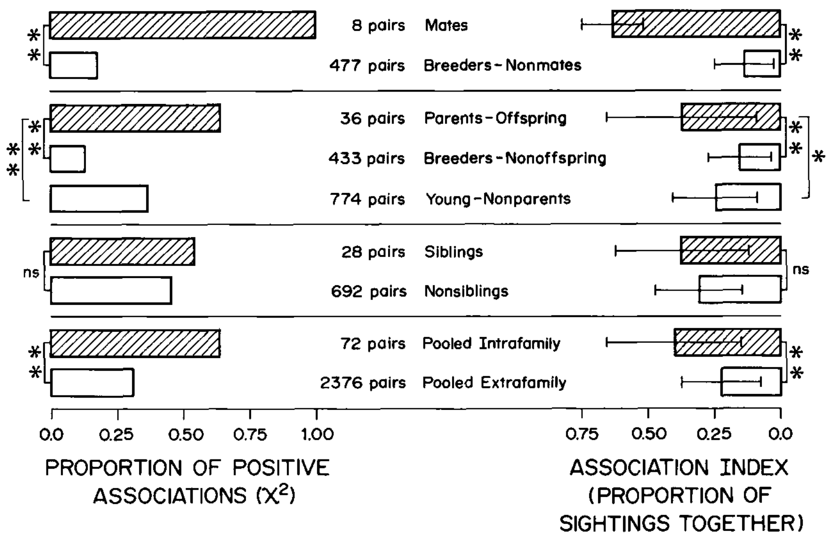

Fig. 1. Left histogram: proportion of significant positive associations (χ^2, $P < 0.05$) within families (shaded bars) and between presumed unrelated (extrafamilial) birds (open bars), by age/status class. ** indicates significant difference in proportions at $P < 0.001$, using test of equality of 2 percentages (Sokal and Rohlf 1969). Right histogram: mean association-index values (±SD) within families (shaded bars) and between presumed unrelated (extrafamilial) birds (open bars), by age/status class. ** indicates significant differences in distributions at $P < 0.001$, * indicates $P < 0.01$ using Kolmogorov-Smirnov 2-sample test (Siegel 1956). ns = not significant.

lationship between offspring and all adults known not to be their parents was similar although not as pronounced (Fig. 1). Associations of young of known nest site with all nonparent adults included 37% positive associations, significantly lower than the comparable parent-offspring proportion. Young birds were found with their parents more often than with other adults.

Parent-offspring associations varied widely among families but were fairly consistent within families (Table 2). Within two families identified as TB and AH, no significantly positive associations were found in 9 pairings of parents with surviving offspring. To the extent that associations between parents and volant young represent the degree of postfledging parental care, these two breeding pairs invested little if anything in their young after fledging. Their overall reproductive success perhaps reflects the cost of not maintaining contact with offspring; 13 young fledged at these two nests over 4 yr, but only 6 (46%) were known to have survived more than 2 months after fledging. The remaining families showed positive associations in 23 of 27 (85%) parent-surviving offspring pairings during all postfledging appearances in groups (Table 2). They also had significantly greater postfledging survival (26 of 28, or 93%, were known to have survived more than 2 months past fledging) when compared with the two families with low parent-offspring association (χ^2, $P < 0.01$). I know little about the associations of parents with young that disappeared within 2 months of fledging because I do not have the requisite 10 resightings for these offspring. These calculations are based only on associations of parents with surviving offspring. For the two families with low associations between parents and surviving offspring, I assume these parents treated their nonsurviving offspring similarly.

Associations between siblings.—The proportion of positive associations among sib pairs (same- and different-age pairs pooled) was 55%, not significantly different from the 46% positive associations found when known-nest young were paired with all other nonsibling young (Fig. 1). This seemingly low proportion of positive associations among sibs (when compared with other intrafamilial categories) was not affected by separating sibs of different ages. Positive associations occurred in 7 of 12 (58%) same-age sib sets and 8 of 16 (50%) different-age sib sets.

TABLE 2. Fledgling survivorship and strength of parent-offspring association.

		Association measures[a]				
		No. of χ^2 values that were:			Dice's index	
Family code	Proportion of fledglings surviving	Significantly positive	Positive	Negative	Mean	SD
LA	6/6	6	2	0	0.329	0.182
DC	4/6	1	1	0	0.331	0.063
ML	6/6	6	0	0	0.550	0.275
LE	7/7	6	0	0	0.664	0.149
SA	3/3	4	1	0	0.422	0.274
TB	2/5	0	2	1	0.116	0.102
AH	4/8	0	0	6	0.000	0.000

[a] Parents with surviving offspring.

In fact, young birds showed strong positive associations regardless of relatedness. Young apparently make no active attempt to follow or remain with their siblings as long as they are with a group of young vultures.

Pooled intrafamilial associations contained a higher proportion of positive associations than did pooled extrafamilial associations (Fig. 1). Overall, immediate family members occurred with each other in communal roosts and feeding groups outside the breeding season more often than they occurred with other presumably unrelated individuals. High intrafamilial associations, however, resulted primarily from parent-offspring and mated pair associations, rather than sibling associations.

Associations between neighbors.—All marked breeding adults of known nest site were tested in pairs with all other nonmate breeding adults of known nest site for association, excluding the months of March, April, and May. Of 82 pairs, 28 (34%) had positive associations, more than the 18% positive associations between breeding adults and all extrafamilial adults (Table 3). However, the proportion of positive associations among neighbors was less than among mates (Table 3). Closer inspection reveals that some breeding pairs associated strongly with certain other pairs. Furthermore, because parents and offspring showed significant levels of association, entire family groups from different nest sites were positively associated. Levels of associations between neighboring breeding pairs could be a function of distance between nest sites. This would imply passive co-occurrence due to degree of home-range overlap in animals restricting their movements to the vicinity of their nest sites. There was no correlation between degree of associations and distance between nest sites within the study area (Fig. 2). A linear regression of mean V values for each distance against distance between nest was not significant ($r = -0.105$, $P \gg 0.05$).

TABLE 3. Comparison of associations between breeding adult Black Vultures and other adults.

	Measures of association				
	χ^2 tests[a]		Dice's index		
Type of association	n	p	n	$\bar{x}$	SD
Breeding adults with all nonmate adults	477	0.182	478	0.135	0.115
	($P < 0.01$)[b]		($D = 0.275$, $P < 0.001$)[c]		
Breeding adults with neighboring breeders	82	0.341	86	0.273	0.210
	($P < 0.001$)[b]		($D = 0.520$, $P < 0.05$)[c]		
Within mated pairs	8	1.000	8	0.628	0.115

[a] n = number of dyads, p = proportion of associations that were significantly positive ($P < 0.05$).

[b] Test of equality of two percentages (Sokal and Rohlf 1969).

[c] Kolmogorov-Smirnov two-sample test (Siegel 1956); D = greatest interval difference between two cumulative frequency distributions.

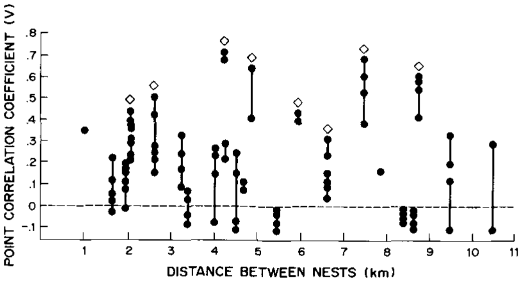

Fig. 2. Point correlation coefficient (*V*) for all breeding adults paired with nonmate locally breeding adults by distance between nests. *V* values for each nest-nest comparison (nest A adults paired with nest B adults) are connected by vertical lines. Diamonds indicate nest-nest comparisons in which all pairs are significantly positively associated (χ^2, $P < 0.05$).

TABLE 4. Occurrences of behavioral interactions between different classes of Black Vultures.

	No. of cases involving:			
Type of behavior	Mates	Parents/offspring	Siblings	Extrafamily
Mutual allopreening	27	26	8	9
Postfledging feedings	0	41	0	0
Interference at roost	2	2	2	0
Interference at food	3	7	0	0

Comparisons of association measures.—All results from Dice's association index agreed with results of Chi-square tests (Fig. 1). Association-index values were greater among mates than unmated adults, and among parent-offspring pairs than among both parent-nonoffspring young and offspring-nonparent adults. Index values did not differ significantly between pairs of sibs and pairs of nonsibling young. Pooled intrafamilial association-index values exceeded extrafamilial values. Association indices between neighboring breeding adults (extrafamilial neighbors) were less than between mates (Table 3), but greater than between breeding adults and all nonmate adults (extrafamilial adult population) (Table 3).

Behavioral correlates of family associations.—Behavioral correlates of family associations include allopreening, feeding, and defending family members against attacks by unrelated birds. Of 70 mutual allopreening interactions involving at least one known family member in communally roosting or feeding groups, 61 were between family members (Table 4). Of the 9 instances of extrafamilial allopreening, 7 involved young birds with other unrelated young (with whom they were positively associated), and 2 involved breeding adults mutually allopreening with adults from neighboring nest sites (with their mates present in both cases). Although most extrafamilial observations were of young allopreening unrelated young, young apparently do not allopreen other young indiscriminately with regard to relatedness. Allopreening between sibs was more common than expected, based simply on the representation of sibs in the population of young birds ($\chi^2 = 66.87$, $P < 0.001$).

Forty-one postfledging feedings involving known parent-offspring pairings were observed. These feedings occurred as late as 8 months after fledging. Adults were never observed to feed young other than their own in spite of begging attempts by other young. Unrelated young attracted by conspicuous regurgitative feeding were always driven away by pecks from the feeding adult.

Central to the association of kin in Black Vultures is the fact that individuals will come to the aid of kin that are being actively displaced or physically attacked by unrelated birds. Although only 16 instances were observed, all involved intercession on behalf of known family members (Table 4).

Family gatherings at nest sites.—In addition to preferring the company of kin and behaving preferentially toward them in communal situations, Black Vultures rendezvous with family members at their unique nest sites. After fledging, young birds that become separated from their parents meet them back at their nest sites. Preening and feedings take place there before birds depart for the evening communal roost. In 188 midafternoon nest-site observations after August fledging through the end of December, at least one family member was present in 101 cases. Both adults and young (at least one of each) were present in 62 cases, and all four nuclear family members were present in 34 cases. In some of the meetings of an entire family, the four members arrived together from the same direction, whereas in other meetings some or all members arrived singly. Nest-site rendezvous of families probably occur daily for about 3 months after fledging and decline slowly in frequency thereafter. By 5 months after fledging, young were no longer observed at the nest sites, and meetings of family members other than mates occurred at roosts and feeding sites.

Courtship and copulation.—Courtship and copulation did not occur in communal situations. Male Black Vultures have a characteristic courtship posture that immediately precedes copulation and is presented to the female at the nest site. I have witnessed 4 copulations; each was preceded by the courtship posture and occurred at the nest site. On only 7 occasions during hundreds of hours of roost and feeding observations during February and March (eggs are laid in mid-March) have I seen birds assume the male courtship posture. In these 7 instances, the posturing bird was approached quickly by several nearby birds of both sexes that began pecking and biting him violently until he fled the area.

DISCUSSION

In their lifetimes, Black Vultures may use many communal roosts. At any one roost the composition of individuals changes nightly, resulting in large-scale mixing of individuals. Nonetheless, family members maintain close contact outside the breeding season in communal feeding and roosting groups. A significantly greater proportion of positive associations involved mated pairs and parent-offspring pairs than their extrafamilial pairings, and pooled intrafamilial associations contained a greater proportion of postive associations than pooled extrafamilial associations.

Young birds, in general, have more positive extrafamilial associations than do their parents. This age difference in association patterns may be partially explained by differential movement rates and the relative site fidelity of young birds during the winter (Rabenold MS). Black Vultures form larger roosting groups during winter than summer. The winter roosting sites are stable within a winter, although smaller satellite roosts occasionally may be used. Turnover rates for adults are greater than turnover rates for young birds at the winter roost, and young birds are more likely to return after an absence. Young birds evidently tend to wait at the winter roost, whereas adults (including their parents) circulate among several roosts. This tendency for young birds to congregate regularly at a single site leads to high association values among regular visitors to the roost, primarily young birds, and accounts for the high proportion of positive associations among unrelated young (Fig. 1) and the higher overall proportion of positive extrafamilial associations involving young from known nest sites (41%) compared with that of their parents (16%) (Fig. 1, $P < 0.05$).

Factors favoring maintenance of contact among family members.—High association between mates would be expected in animals that are highly gregarious immediately preceding and during courtship and egg-laying, when mate guarding might be necessary. However, in Black Vultures mates are highly associated year-round (except during incubation and brooding, when they take alternate nest shifts), with no marked increase immediately preceding reproduction. Although mate guarding could contribute to high association during the reproductive period, courtship and copulation do not occur in communal situations, but are confined to the nest site and isolated from other birds. Because birds adopting the courtship posture in groups are attacked by nearby birds, strict mate guarding by individual males is unnecessary.

Parent-offspring bonds persist in part because of extended postfledging dependence of young on direct parental feeding. Families with low parent-offspring association had lower fledgling survivorship than those with high parent-offspring association. Regurgitative feedings of offspring fledged in August occurred as late as the following April. During this period young birds will not compete for food at a carcass attended by many adults. They wait at the side for their parents to emerge, then beg loudly for regurgitative feedings. The postfledging nest-site rendezvous underscore the dependence of young on parents for feedings and feeding assistance in groups. Although family members, and especially young birds, often become separated in hectic morning roost departures, daily reassembly at nest sites assures that family members maintain contact during the period when young are dependent on parents for feeding and still unfamiliar with many parts of their ranges. During their first spring (almost 1 yr old) young birds begin to join large feeding groups, and their parents aid them by threatening other adults that attempt to drive these offspring away from food. This form of assistance has been documented in other species with long-lived associations between parents and young (Scott 1980). As juveniles mature and become more competitive feeders, the relationship with their parents may evolve into mutual aid-giving during competition within a large feeding group. That parent-offspring associations persist well beyond the age of strict dependence suggests that long-term associations continue to be mutually beneficial.

Aid in feeding may be the largest single factor favoring retention of strong ties among members of Black Vulture families. Associations of family members remained high when feeding observations alone were considered, while extrafamilial associations fell to the level expected from random assortment. Because their food supply is extremely patchy in space and time, an individual's chances of finding food while alone may be small, and competition at feeding sites can be fierce. Because a single source usually contains enough food for several birds, a finder should recruit his family members preferentially to share food with them, thereby increasing his inclusive fitness by fostering survival of genetically correlated individuals (Hamilton 1964). In addition, a coalition of individuals may better defend a small carcass or part of a large one. As a consequence, each may feed better than if competing alone.

Are associations based merely on range overlap?—If young birds cover large ranges centered on their natal nest sites until they become reproductive and adults center their ranges on their breeding sites, immediate family members would have extensive or complete range overlap. Although their ranges would overlap extensively with many other individuals' ranges, family members would have stronger associations with closely related birds than with others simply as a result of passive association from sharing an identical range, even if the birds moved independently of each other within this range. Extrafamilial association values should vary widely depending on the extent of range overlap, which may be correlated with the distance between nest sites. Mates would have the highest associations, followed by neighboring breeding adults, followed by nonmate adults, including all adults regardless of nest site. These predictions match my results (Table 3). However, within the neighbor-neighbor pairs, association values should decline with increasing distance between nest sites; those nesting closer together might have more extensive range overlap than those nesting farther apart. No such relationship was evident when the association values of breeding adults nesting within this study area were plotted against distance between nest sites (Fig. 2). It appears instead that some families have strong alliances with others and that this pattern of alliances between families is not a function of distance between nest sites.

It is possible, however, that the greatest internest distance considered (<11 km) is trivial to a vulture and that it is not surprising, therefore, that associations tend to be high with no significant decline over this distance. My observations of breeding adults suggest that their movements are heavily concentrated within 20 km of their nest sites throughout the year. Within this restricted range, internest distances approaching 11 km include a significant portion of the estimated range of breeding adults. Furthermore, the daily afternoon meetings at nest sites make it unlikely that families would travel great distances out of the study area. If greater internest distances were considered, a decline in associations might be found that would support the passive range-overlap hypothesis. Associations must decline with increasing internest distance. Despite its potentially large range, an individual bird covers a finite area, and associations must eventually fall to zero. It is therefore of interest to look not only for a decline in associations with distance, but at the range of association values within a reasonable distance from each family's nest site. The passive range-overlap hypothesis predicts a smooth decline from center of range to edge. Not only was no decline found, but association values at each internest distance varied widely (Fig. 2); negative association values were found at even very small internest distances. In fact, for only one family was the most closely associated family found at the next-nearest nest site.

The lack of correlation between associations and internest distances suggests that particular associations, both at family and neighborhood levels, are based on some attribute of the birds other than wide overlap of ranges. The active nature of intrafamilial associations is also supported by conspicuous allopreening and intercessions in fights. Because intrafamilial association is so marked, it may be that breeding adults of highly associated families are also closely related. Although no birds marked as nestlings have bred in the study area, 3- and 4-yr-old birds are still in the area and use local roosts. Age of first breeding is not known for this species. If many birds breed in their natal area and intrafamilial associations persist, it is likely that neighbors may include parent-offspring or sibling relationships.

Roosts as information centers.—Perhaps the chief theoretical criticisms of Ward and Zahavi's (1973) information-center hypothesis is that it relies on reciprocation between finders and followers. Unless reciprocation is assured, the participation of successful foragers appears paradoxical. Why should they return, only to be followed by competitors, unless there is a yet stronger advantage in joining an aggregation, such as reduced risk of predation (Alexander 1974, Hoogland and Sherman 1976)? A common assumption is that food is sufficiently abundant within a patch that competition would be weak and attempts to dissuade followers would be pointless (Krebs 1978). However, there must be a maximum number of followers beyond which this would not be true. Furthermore, the field evidence in support of this hypothesis has to date been gathered on colonially breeding birds (Krebs 1974, Erwin 1978, Waltz 1981), in which successful foragers must eventually return to feed young. In these cases, predator defense or localized nesting sites become particularly plausible explanations for aggregation. Black Vultures have no known predators as adults and thus represent a fairly simple system for examining certain aspects of the information-center hypothesis. Because they are not colonial breeders, members of the population that are vulnerable to predation (nestlings) are not present in the aggregations. Also, successful foragers need not return to a specific aggregation site to feed nestlings and they could conceivably avoid competitors by sleeping alone, although I have no evidence that such "cheating" occurs. While a single bird roosting solitarily would be difficult to detect, I have many examples of birds seen at carcasses joining a roosting group the same evening (Rabenold MS).

The paradox of the returning successful forager is partially resolved if it returns to lead its family members to food. But why should families not maintain separate fixed aggregation centers (such as their nest sites) to which they return with foraging information to avoid sharing with nonrelatives? If the food supply is sufficiently patchy, entire families could search without success, and they could then rely on the larger group for foraging information. Even if they are followers, cooperation of entire families in competitive groups may increase their chances of feeding. If families or larger alliances of families function as units competing for food, no one nest site would provide a suitable meeting place. Families could instead meet allies and relatives at neutral roost sites. Beyond the observations reported here of family members aiding each other in roosting and feeding interactions, detailed observations of feeding interactions are needed to verify the competitive advantage of individuals feeding in the presence of family members or allies.

The evidence reported here suggests that Black Vulture communal roosts serve as meeting places for family groups and allied families. Family members associate with each other preferentially and assist each other in competitive interactions in large roosting and feeding groups. The extent to which kin selection has shaped the evolution of communal roosts in Black Vultures cannot be estimated without greater knowledge of the relatedness of allied family groups. If young birds eventually breed near their natal areas and family bonds persist, allied neighbors may also be closely related. The possibility that large roosting groups consist of a few large extended family units or clans is intriguing in light of the information-center hypothesis. This study demonstrates positive associations and cooperative behavior among family members, and I show elsewhere (Rabenold MS) that following from the roost and continued participation in a roost might be discouraged in unrelated birds by aggressive interactions in the roost. While these results do not present direct evidence that foraging information is transferred at roosts, they suggest that potential recipients of information are often family members, a condition under which the evolution of information sharing is more likely than among birds assorted randomly with respect to relatedness.

ACKNOWLEDGMENTS

This work was supported in part by a grant from the Frank M. Chapman Fund of the American Museum of Natural History and in part by a UNC Research Fellowship. The cooperation of local landowners, especially the A. J. Perry family and the entire Lindley clan, is greatly appreciated. Celia Lewis was an untiring assistant in all phases. B. Brown, S. Campbell, C. Christensen, K. Long, K. Meyer, H. Mueller, B. Simpson, M. Wallace, and especially P. Frederick and K. Rabenold helped in various phases of the fieldwork. E. Patterson and B. Bromer wrote and rewrote many computer programs. The manuscript has profited considerably from comments by J. A. Jackson, H. C. Mueller, K. N. Rabenold, R. H. Wiley, E. C. Waltz, and a very helpful anonymous reviewer. I especially thank my major professor, H. C. Mueller, for guidance and encouragement.

LITERATURE CITED

ALEXANDER, R. D. 1974. The evolution of social behavior. Ann. Rev. Ecol. Syst. 4: 325-383.

DICE, L. R. 1945. Measures of the amount of ecologic association between species. Ecology 26: 297-302.

ERWIN, R. M. 1978. Coloniality in terns: the role of social feeding. Condor 80: 211-215.

HAMILTON, W. D. 1964. The genetical evolution of social behavior. J. Theoret. Biol. 7: 1-52.

HOOGLAND, J. L., & P. W. SHERMAN. 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. Ecol. Monogr. 46: 33-58.

JACKSON, J. A. 1975. Regurgitative feeding of young Black Vultures in December. Auk 92: 802-803.

KREBS, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardea herodias*). Behaviour 51: 99-134.

———. 1978. Colonial nesting in birds, with special reference to the Ciconiiformes. Pp. 299-314 *in* Wading birds (A. Sprunt, J. C. Ogden, and S. Winckler, Eds.). New York, Natl. Audubon Soc. Res. Rept. No. 7.

MCHARGUE, L. H. 1977. Nesting of Turkey and Black vultures in Panama. Wilson Bull. 89: 328-329.

PIELOU, E. C. 1976. Mathematical ecology. New York, Wiley.

RABENOLD, P. P. 1983. The communal roost in eastern cathartid vultures—an information center? Pp. 303-321 *in* Vulture biology and management (S. R. Wilbur and J. A. Jackson, Eds.). Los Angeles, Univ. California Press.

REEVES, T. L., M. BLAIR, J. O. FEARRINGTON, B. HORNY, & T. TALLEY. 1970. Land development potential study. Prepared for the County of Chatham, North Carolina. HUD Project #NCP77.

SCOTT, D. K. 1980. Functional aspects of prolonged parental care in Bewick's Swans. Anim. Behav. 28: 938-952.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. New York, McGraw-Hill.

SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. San Francisco, W. H. Freeman.

WALLACE, M. P., P. G. PARKER, & S. A. TEMPLE. 1980. An evaluation of patagial markers for cathartid vultures. J. Field Ornithol. 51: 309-314.

WALTZ, E. C. 1981. The information center hypothesis and colonial nesting behavior. Unpublished Ph.D. dissertation, Syracuse, State Univ. New York Coll. Env. Sci. and Forestry.

———. 1982. Resource characteristics and the evolution of information centers. Amer. Natur. 119: 73-90.

WARD, P., & A. ZAHAVI. 1973. The importance of certain assemblages of birds as "information-centres" for food-finding. Ibis 115: 517-534.

COMPARATIVE REPRODUCTIVE SUCCESS OF YELLOW-SHAFTED, RED-SHAFTED, AND HYBRID FLICKERS ACROSS A HYBRID ZONE

WILLIAM S. MOORE[1] AND WALTER D. KOENIG[2]

[1]*Department of Biological Sciences, Wayne State University, Detroit, Michigan 48202 USA, and*
[2]*Hastings Reservation and Museum of Vertebrate Zoology, University of California,*
Star Route Box 80, Carmel Valley, California 93924 USA

ABSTRACT.—Alternative hypotheses of hybrid zones make specific predictions about reproductive components of fitness in the hybrids. The dynamic-equilibrium and reinforcement hypotheses are premised on reduced hybrid fitness, which should be apparent as reduced clutch or brood size or as increased embryonic mortality. The hybrid-superiority and introgression hypotheses predict normal clutch and brood size and embryonic mortality.

Reproductive success was measured at four study sites on a transect across the hybrid zone between the Yellow- (*Colaptes auratus auratus*) and Red-shafted (*C. a. cafer*) subspecies of the Northern Flicker. Two additional clutch size samples representing pure Yellow- and Red-shafted flickers were obtained from museum egg collections. Mean clutch size did not differ significantly among the six samples. Factorial ANOVAs showed that early clutches and broods are larger than late clutches and broods, but no significant difference was detected between hybrid and parental study sites. Analyses of the effect of phenotype (yellow-shafted, red-shafted, hybrid) also suggest that neither clutch size nor brood size is affected, with the exception that hybrid males sired significantly smaller broods. Finally, there were no significant effects of type of cross (red-shafted male × hybrid female, etc.) on the ratio brood-size/clutch-size.

The only evidence for reduced hybrid fitness was in the test where males with hybrid phenotypes appear to have sired small broods. This may indicate that abnormal behavior of hybrid males affects female fecundity, but it is also plausible that this marginally significant result is a type I statistical error. The overall lack of evidence for reduced hybrid fitness is inconsistent with either the dynamic-equilibrium or reinforcement models. Of the two remaining alternatives, the bounded hybrid-superiority model appears the more likely explanation of the Northern Flicker hybrid zone because earlier work (Moore and Buchanan 1985) showed that the hybrid zone is not becoming broader, as predicted by the introgression model. *Received 20 February 1985, accepted 2 July 1985.*

HYBRID zones often occur between avian populations that have diverged to near the species level but retain contiguous distributions as a result of either secondary contact or parapatric divergence (Short 1969, Moore 1977, Rising 1983a). Typically, hybridization is rampant in the zone but the zone itself is very narrow and seems to act as a barrier separating markedly divergent plumage patterns or song types, or both. Furthermore, the biogeography of most avian hybrid zones suggests that they arose in antiquity, probably as a result of Pleistocene glaciation, and therefore seem to be evolutionarily stable configurations (Short 1970, Moore 1977; but see Barrowclough 1980).

Three theories have been proposed to explain the existence of stable hybrid zones. Moore (1977) suggested that hybrid zones represent secondary contacts between taxa that had diverged in isolation but not to the extent that hybridization would disrupt distinctly coadapted gene complexes resulting in hybrid breakdown or hybrid unfitness. He further suggested that the secondary contact was established as distinct ecological communities expanded from refugia to form a "suture zone" in the sense of Remington (1968) and that the genes of the divergent characters are either adapted in their respective communities or closely linked to genes that are. The hybrid zone persists, then, because it occurs in an ecotone in which neither parental taxon is particularly well adapted. This was termed the hybrid-superiority model, although *bounded* hybrid superiority is more apt because it implies that hybrid superiority is restricted geographically.

Barton (1979) and Barton and Hewitt (1981) developed an alternative hypothesis that explains stable hybrid zones by balancing opposing forces. The essential feature of the Barton-Hewitt *dynamic-equilibrium model* is hybrid unfitness, which prevents the hybrid zone from becoming broader through introgressive hybridization; less-fit hybrids form a narrower hybrid zone. Barton (1979) showed that hybrid unfitness itself can fix the width of the hybrid zone and further showed that variations in population density could prevent the hybrid zone from "flowing" geographically.

The third alternative is that the hybrid zone appears stable only to a short-lived observer but actually is growing broader through introgressive hybridization or becoming more restricted as premating reproductive isolation is reinforced by selection against hybrids (Wilson 1965, Remington 1968). Whether introgression or reinforcement is expected would depend on whether hybrid phenotypes are at least as fit as the parental phenotypes or less fit, respectively.

The three alternatives provide radically different explanations of hybrid zones, each with its own implications for speciation theory. Furthermore, the alternatives appear to be testable, as the dynamic-equilibrium and reinforcement models predict some measure of hybrid breakdown, whereas the hybrid-superiority and introgression models do not. More precisely, according to the dynamic-equilibrium and reinforcement models, one would expect increases in infertility and development aberrations in hybrid phenotypes. The pairs of alternatives can be tested further by studying the historical stability of the hybrid zone.

The idea that hybridization between distinctly coadapted gene pools results in hybrid breakdown is an old idea in evolutionary biology that is of particular importance to speciation theory. Collectively, the assorted maladies that are expected to result are termed postmating reproductive isolating mechanisms. Although hybrid breakdown could manifest at any stage in the life cycle, the maladies most often mentioned affect the early development or fertility of hybrid phenotypes. Thus, where natural hybridization has disrupted coadapted gene complexes, one would expect higher frequencies of developmental anomalies and reduced fertility. In birds this should appear as reduced brood and clutch sizes, respectively.

We report clutch- and brood-size data for four populations of the Northern Flicker (*Colaptes auratus*) along a transect across the hybrid zone between the Yellow- and Red-shafted flickers (*C. a. auratus* and *C. a. cafer*) in western Nebraska and eastern Wyoming. The two central locales support hybrid populations, whereas the distal locales represent parental populations (see Fig. 1). Our purpose is to determine whether hybridization between these well-marked subspecies has disrupted coadapted gene complexes and whether hybrid breakdown is essential to understanding this hybrid zone. Data pertaining to historical stability were reported earlier (Moore and Buchanan 1985).

The structure of the hybrid zone has been reported by Short (1965) and Moore and Buchanan (1985). To summarize briefly, the Yellow-shafted Flicker is broadly distributed in diverse woodland types across eastern North America, whereas the Red-shafted Flicker is the western North American counterpart. The hybrid zone occurs on the western Great Plains, primarily in riparian woodlands (cottonwood, peach-leaved willow, and green ash) but also in the coniferous forests of the Black Hills, the Pine Ridge region of Nebraska and South Dakota, and in the Cypress Hills of Saskatchewan. The hybrid zone may be continuous in the solidly forested montane regions of Alberta, British Columbia, and southern Alaska (Short 1965, Moore pers. obs.). The two subspecies exhibit contrasting conditions for 6 (5 in females) plumage characters; e.g. red-shafted males have a red malar stripe, whereas that of the yellow-shafted is black. Hybrids exhibit intermediate variations. These characters are easily scored, even with binoculars. Mating is random with regard to the plumage characters (Short 1965, Bock 1971, Moore and Buchanan 1985). The hybrid zone varies in width and is asymmetrical, with introgression evident farther west of center than east (see Fig. 1). Population densities are uniformly high along the study transect (Moore and Buchanan 1985).

MATERIALS AND METHODS

Active nests were located throughout May and June in 1981–1984 at four study sites on a transect across the hybrid zone (Fig. 1). The study sites are: Sutherland (James Haugland farm on the south bank of the South Platte River between the river and interstate highway I-80, 1.75 km south-southeast of Sutherland, Lincoln Co., Nebraska, R33W, T14N, secs. 32, 33); Bridgeport (Blanchard-Lindgren ranch on the

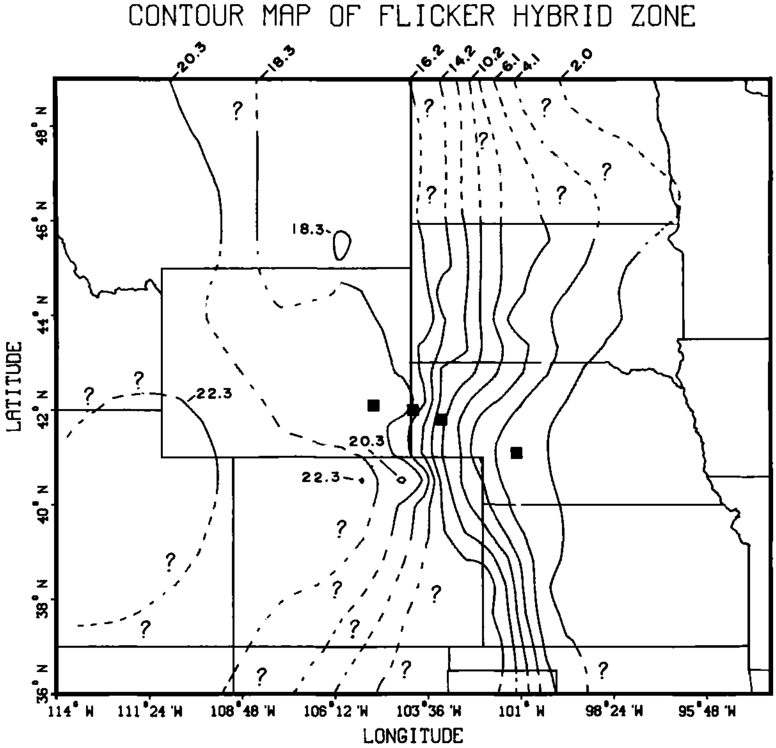

Fig. 1. Provisional contour map of the Northern Flicker hybrid zone on the western Great Plains. The solid squares mark the four live-study sites (from east to west: Sutherland, Bridgeport, Morrill, and Wheatland). The contour levels indicate the transition in Short's (1965) hybrid index (HI) from yellow-shafted in the east (HI = 0) to red-shafted in the west (HI = 23). The dashed contours and question marks indicate poorly collected areas that cannot be accurately mapped. The map is accurate in the region of the live-study sites.

south bank of the North Platte River, 7.5 km west-northwest of Bridgeport, Morrill Co., Nebraska, R51W, T20N, secs. 21, 22, 23); Morrill (north bank of the North Platte River, 4.8 km west-northwest of Morrill, Scottsbluff Co., Nebraska, R58W, T23N, secs. 13, 14); and Wheatland (Laramie River at the confluence of Sybille Creek, 13 km west-northwest of Wheatland, Platte Co., Wyoming). Bridgeport and Morrill were established as study sites in 1981; Sutherland and Wheatland were not established until 1982.

Nest cavities were reached with the aid of a 9.6-m extension ladder and climbing gaffs where necessary. Cavity interiors were viewed with a 6-cm circular mirror on a handle and a penlight.

The following data were collected for each nest: score for each plumage character for both parents (see below), clutch size, brood size, and, when possible, date when the first egg was laid.

Clutch size.—It was necessary to establish that the clutches were complete at the times of the final counts. With rare exceptions, flickers lay one egg per day (Sherman 1910, Moore pers. obs.). To establish completeness, the eggs in a given nest were counted over several days as laying progressed and incubation began. When clutch size remained the same for at least two successive days, the clutch was considered complete. In some cases it was apparent that the clutch was complete at the time the nest was discovered because clutch size did not increase or the eggs hatched in less than 11 days, the normal incubation period for flickers (Sherman 1910, Moore pers. obs.).

Brood size.—An access port was cut into the nest cavity during the brooding period. At that time, the hatchlings were banded and counted, and the adults were trapped, banded, and scored phenotypically. Usually, the access port was cut and the hatchlings banded in the afternoon of one day, and the adults were trapped the following morning. Adults were trapped in the nest cavity by a remote-activated trap door modified from a common rat trap. The trapped adult was then removed through the access port. Follow-up observations on numerous nests suggest that the trapping and banding activities did not permanently disrupt the nesting process; nevertheless, brood size was based on the number of hatchlings in the nest at the time it was first disturbed rather than the number that subsequently fledged. The ages of the broods at the time hatchlings were counted varied between 10 and 17 days after hatching.

In most cases, Short's (1965) hybrid index (HI) was determined for both adults at the time the nest was discovered. This initial phenotypic determination was done by observing the adults around the nest with binoculars. In those cases where the adults were subsequently trapped, the HI was redetermined on the bird in hand. Priority was given to HIs determined on hand-held birds, but in some cases when it was not possible to trap one of the adults (usually the female), the HI determined using binoculars was used. The concordance between scores determined using binoculars and in the hand was strong.

Short's (1965) hybrid index is based on 6 plumage characters in males. The 6 characters are listed according to the following format: character (abbreviation, *auratus*/*cafer*), where *auratus* and *cafer* represent the relative states for the parental subspecies. The plumage characters are: crown color (CROWN, gray/brown); ear covert (EAR, brown/gray); throat color (THROAT, brown/gray); red nuchal patch (NUCHAL, present/absent); shaft color (SHAFT, lemon-yellow/salmon-red); and malar stripe (MALAR, black/red). All of these characters except MALAR can be scored in females; females lack the malar stripe. Each character is given an integer score on the scale 0–4, where 0 and 4 represent the *auratus* and *cafer* parental states, respectively, and the integers 1–3 represent proportionally intermediate conditions. In theory, then, pure *auratus* males and females would have HIs of 0, and *cafer* males and females would score 24 and 20, respectively. In practice, however, CROWN scores are never higher than 3 in this portion of the species range. We reserved the score of 4 for the deeper brown crown color of the northwestern race (Short 1965), but this variation appears unrelated to hybridization. In any case, pure red-shafted males and females would have hybrid indices of 23 and 19, respectively, at the latitude of our transect.

Because some nests were depredated after clutch size was determined and others were found after the eggs hatched, there is variation in sample size for clutches and broods. Sample sizes are given in the results section in the context of specific tests. SPSS (release 9.2) was used to perform statistical tests (Nie et al. 1975).

Sutherland and Wheatland were intended to serve as yellow-shafted and red-shafted reference samples, respectively. However, there is some evidence of introgression at both localities. Two additional reference samples were extracted from the clutch-size data compiled by Koenig (1984). One sample represents pure yellow-shafted and includes clutches within the block delineated by longitudes 89–96°W and latitudes 38–42°N; the second sample includes clutches within longitudes 105–113°W and latitudes 38–42°N. These two blocks are roughly contiguous with the eastern and western ends of the study transect; they are narrow so as to avoid variance resulting from the strong latitudinal gradient in clutch size in *Colaptes* (Koenig 1984). Koenig's data were extracted from the egg collections of museums, and we followed his protocol for determining the completeness of clutches. Only clutches where incubation was evidenced by embryonic development were included in our samples.

TABLE 1. Average hybrid index scores, percentage transition from pure yellow-shafted (0%) to pure red-shafted (100%) scores, and sample sizes (*n*) on a transect across the Northern Flicker hybrid zone.

	Average hybrid index		Percentage of pure red-shafted score	
Study site	Female (*n*)	Male (*n*)	Female	Male
Sutherland	0.73 (11)	0.69 (13)	3.8	3.0
Bridgeport	4.85 (26)	7.09 (32)	25.5	30.8
Morrill	13.64 (25)	16.22 (27)	71.8	70.5
Wheatland	15.71 (14)	18.19 (16)	82.7	79.1

RESULTS

Phenotypes of adults at the four study sites.—The average hybrid index (HI) scores for nesting adults at the four study sites are presented in Table 1. The two end sites, Sutherland and Wheatland, ideally represent pure yellow- and red-shafted locales for comparison with the hybrid locales, Bridgeport and Morrill. Sutherland is close to pure yellow-shafted, but significant numbers of hybrid phenotypes are included in the Wheatland samples. For this reason and because sample sizes from Wheatland are small, greater consideration should be given to Sutherland as a parental population for comparison.

Descriptive statistics.—The distributions of clutch and brood sizes for the six samples are illustrated in Fig. 2, along with the means, standard deviations, and sample sizes. Brood-size data were not available for pure red- and yellow-shafted samples based on museum egg collections and so only clutch-size data are given for these samples.

The distributions of clutch and brood sizes at all locales appeared sufficiently close to normal distributions that parametric statistical tests

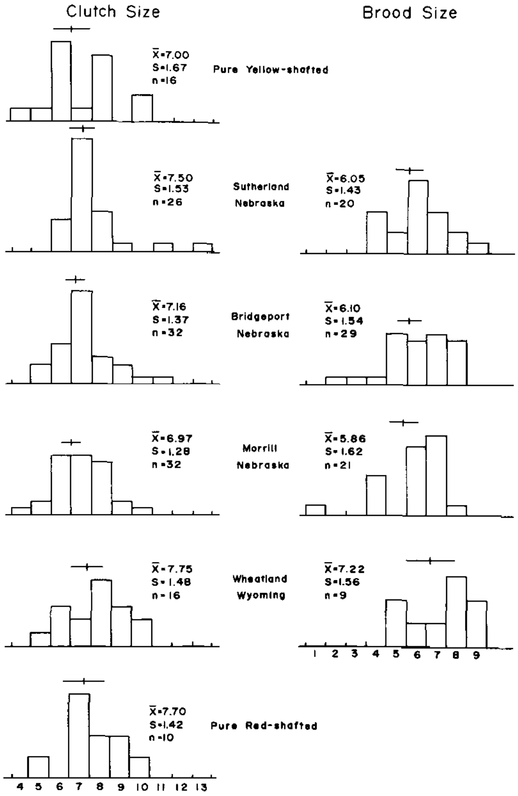

Fig. 2. The distributions of clutch and brood sizes across the Northern Flicker hybrid zone. The extreme upper and lower clutch panels are based on museum egg collections; the other distributions are based on the four live-study sites. The horizontal line above each histogram is a 95% confidence interval centered at the mean.

were valid in most instances and provided more sensitive statistical tests than did corresponding nonparametric tests.

Clutch-size comparisons across study sites.— Variances in clutch size were homogeneous across the four study sites and two museum samples (Bartlett-Box *F*-test, $P < 0.87$). This is of interest because disruption of coadapted gene complexes via hybridization might be expected to increase variance in clutch size. Although not significant, clutch-size variances were lowest at the two hybrid locales. Because the variances were homogeneous, we compared mean clutch size across locales by completely randomized-design ANOVA. In this analysis, the mean clutch size did not differ significantly in any of the six samples ($P < 0.363$).

As the data were collected from the four live-study sites, it seemed as though clutch sizes of early-nesting pairs were larger than those of late nesters and that there was also variation between years. Uncontrolled sources of variance could obscure any underlying difference between locales or alternatively could bias the test. We tested for the effects of seasonal variation (early vs. late clutches) and between-year variation by a factorial ANOVA with site (1–4), season (early, late), and year (1982, 1983, 1984) as factors.

Three problems in the design of this three-factor ANOVA should be mentioned. First was how to separate early and late clutches. We plotted a histogram of first-egg dates. A conspicuous bimodality was manifest, with a valley around 20–21 May. This is consistent with the field observation of a period in late May during which new nests are more difficult to find than earlier or later. Thus, two levels were defined for the factor season; early comprises nests in which laying began 20 May and earlier, and late comprises nests in which laying began 21 May and later. The second problem is that Sutherland and Wheatland were not established as study sites until 1982; thus, data are available at Bridgeport and Morrill for 4 yr, 1981–1984, but for only 3 yr at Wheatland and Sutherland. For this analysis, then, only the years 1982–1984 were considered. The third problem is that the numbers of observations (clutches or broods) in the 24 cells resulting from the cross classification of the three factors are unequal, which means that the effects are not orthogonal. The regression approach of adjusting sums of squares was used to correct for nonorthogonality (Nie et al. 1975).

The results of this analysis are that the effect of season was very significant ($P < 0.002$), but neither site ($P < 0.382$) nor year ($P < 0.240$) was significant, nor were any of the interaction terms.

Because the factor year was not significant but season was, the most parsimonious ANOVA model for the final comparison of mean clutch size between sites considered just two factors, site and season. In this ANOVA (Table 2), again using the regression approach to correct for nonorthogonality, the effect of season remained significant ($P < 0.001$), with early clutches averaging 7.82 eggs vs. 6.80 for late clutches, whereas the effect of site was even less significant ($P < 0.561$) than in previous tests.

Brood-size comparisons across study sites.—Brood size was analyzed in exactly the same manner as clutch size with similar results. The analysis of clutch size provided no statistical evidence for reduced hybrid fitness, and the brood-size statistics were even less compelling. Mean brood size was actually greater at Bridgeport than Sutherland (Fig. 2), although, again, there were no significantly different means. Brood size was correlated with clutch size ($r = +0.62$, $P < 0.0001$), and so the more refined factorial designs yielded much the same results as the clutch-size analyses, viz., year did not affect brood size but season did ($P < 0.014$). In the two-factor ANOVA, site did not affect brood size ($P < 0.651$).

The analyses of clutch and brood size were similar, but it is important to note that clutch and brood size probably would be affected by different components of fitness. Although abnormal male behavior conceivably could affect the female reproductive cycle (Lehrman 1965), clutch size should be affected primarily by female fertility, whereas brood size could be affected by male fertility as well as zygotic mortality. It is possible to assess the effect of hybridization on development alone by analyzing brood size while statistically controlling for clutch size. This might be accomplished by comparing the slopes of lines of brood sizes regressed on clutch sizes for the four sites by analysis of covariance. However, such an analysis may not be valid; brood sizes are not normally distributed for a given clutch size because in too many cases brood size is equal to clutch size. A cruder but safer test can be accomplished by comparing the ratios of brood-size/clutch-size across sites by the nonparametric Kruskal-Wallis test. The test of the null hypothesis that the central tendencies (means) of this ratio are identical across sites cannot be rejected ($P < 0.485$; sample sizes: Sutherland = 20, Bridgeport = 26, Morrill = 18, Wheatland = 8). Although the validity of an analysis of covariance is suspect, such an analysis gave a very similar result. Thus, there is not evidence of hybrid unfitness in the form of reduced brood size at hybrid locales.

Clutch- and brood-size comparisons by phenotype.—Males and females can be classified as pure yellow-shafted, pure red-shafted, or hybrid based on HI scores. Clutch and brood sizes can then be compared between phenotypic classes as opposed to between locales, as in the previous analysis. Females with HI scores of 3-17 inclusive were classified as hybrids, those with scores <3 as yellow-shafted, and those >17 as red-shafted. For males, individuals scoring between 3 and 21 inclusive were classified as hybrids, those <3 as yellow-shafted, and those >21 as red-shafted.

TABLE 2. The effect of site and season on mean clutch size along a transect across the Northern Flicker hybrid zone.

Source	Sum of squares	df	Mean square	F-statistic	Attained significance
Total	180.39	95	—	—	—
Site	3.63	3	1.21	0.69	$P < 0.561$
Season	22.00	1	22.00	12.52	$P < 0.001$
Site by season	0.12	3	0.04	0.02	$P < 0.995$
Error	154.64	88	1.76	—	—

The results of these analyses are summarized in Table 3. Adults from the four study sites were pooled and reclassified by phenotype. Again, to control the effect of early vs. late nesting, a two-factor ANOVA, season (early, late) × phenotype (yellow-shafted, hybrid, red-shafted), was employed for the comparisons of clutch and brood sizes. However, because there were no data for late broods sired by red-shafted males, the ANOVA of male brood was restricted to two phenotypic classes, i.e. season (early, late) × phenotype (yellow-shafted, hybrid). In the four tests of the effect of phenotype on clutch and brood size, hybrid males sired significantly ($P < 0.04$) smaller broods than nonhybrids; the other three tests were not significant.

This result provided some evidence for reduced hybrid fitness. However, a more detailed examination of this apparent reduction in brood size was enigmatic. Either reduced fertility in hybrid males or increased frequency of developmental abnormalities in zygotes sired by hybrid males may be the cause. In either case, clutch size should *not* be reduced, but the effects should be apparent in a reduced ratio of brood-size/clutch-size. A paradox is then apparent in Table 3 because the brood-size/clutch-size ratio was not significant in itself (Kruskal-Wallis test), and both a reduced clutch size and an increased zygotic mortality seemed to contribute about equally to the statistically significant reduction in brood size. It is possible that

TABLE 3. Average clutch and brood sizes and their ratios for pure Yellow-shafted, pure Red-shafted, and hybrid flickers (sample sizes in parentheses).

	Clutch size		Brood size		
	Early	Late	Early	Late	Brood/clutch
Female phenotype					
Yellow-shafted	7.42 (12)	6.63 (8)	6.11 (9)	5.00 (6)	0.835 (15)
Hybrid	7.84 (25)	6.71 (17)	6.53 (28)	5.83 (12)	0.833 (34)
Red-shafted	7.40 (5)	8.00 (2)	6.80 (5)	6.00 (1)	0.903 (5)
Test					
Phenotype	$P < 0.61$[a]		$P < 0.39$[a]		$P < 0.68$[c]
Season	$P < 0.37$		$P < 0.18$		
Male phenotype					
Yellow-shafted	8.06 (16)	7.50 (2)	7.00 (15)	7.00 (2)	0.898 (16)
Hybrid	7.27 (30)	6.61 (26)	6.14 (28)	5.40 (20)	0.826 (42)
Red-shafted	8.60 (5)	7.00 (2)	8.00 (4)	—	0.866 (4)
Test					
Phenotype	$P < 0.15$[a]		$P < 0.04$[b]		$P < 0.17$[c]
Season	$P < 0.09$		$P < 0.53$		

[a] ANOVA: phenotype (yellow, hybrid, red) × season (early, late).

[b] ANOVA: phenotype (yellow, hybrid) × season (early, late).

[c] Kruskal-Wallis test.

two sampling errors compounded to produce a false rejection of the null hypothesis or, alternatively, that hybrid males somehow affected the egg-laying capacity of their mates—perhaps through behavior (Lehrman 1965).

The effects of particular crosses on hatchling success.—The data set allowed one additional set of tests for reduced hybrid fitness: the effects of specific crosses (e.g. yellow-shafted female × hybrid male, etc.) on clutch and brood size (Table 4). Of the nine possible types of crosses, none involved red-shafted × yellow-shafted and only one involved red-shafted × red-shafted. The average ratio (brood-size/clutch-size) for all nests was pooled from the four sites (Table 4). The ratio for hybrid males weighted and averaged across all types of females was 0.826. The grand mean for all crosses was 0.838. The means (central tendencies) were compared by the Kruskal-Wallis test. The null hypothesis that the sum of ranks for the six classes (excluding the cross where $n = 1$) are identical could not be rejected ($P < 0.336$). Although not significant, the hatchling survival rate (brood-size/clutch-size) was lowest for the cross hybrid × hybrid. A similar analysis was made for clutch size, but there were no significant differences between classes as defined by the type of cross. This is not surprising because the female alone probably determines clutch size.

DISCUSSION

Several points concerning ecologically and geographically adaptive variation in clutch size need to be considered, as they may be confounding our attempt to identify the effects of hybridization (Koenig 1982, 1984). Latitudinal variation across the four study sites, which spanned about 1°, is minimal. According to Koenig's (1984) regression of clutch size on latitude for the Northern Flicker, the expected difference in clutch size between Sutherland and Wheatland is only 0.1 egg. However, ecological differences between study sites may have influenced our results. In particular, there is both an elevational increase from Sutherland (902 m) to Wheatland (1,448 m) and an ecological gradient of increasing aridity and harsher winter conditions. These differences may produce greater seasonality in productivity, found by Koenig to significantly influence clutch-size variation in the Northern Flicker, and thus may be partially responsible for the (nonsignificantly) larger clutch sizes found in Wheatland and in the pure red-shafted samples.

Such an effect is likely to be minimal for several reasons. Winter actual evapotranspirations (AE), defined as the sum for the three consecutive months yielding the lowest AE values, are 0 for all sites (Thornthwaite Assoc. 1964). AE was used by Ricklefs (1980) and Koenig

TABLE 4. Hatchling survivorship as measured by the ratio of brood size to clutch size for various natural crosses from the hybrid zone (sample sizes in parentheses).

	Phenotype of male parent			
	Yellow-shafted	Hybrid	Red-shafted	Weighted mean[a]
Phenotype of female parent				
Yellow-shafted	0.838 (21)	0.823 (12)	—	0.833 (33)
Hybrid	0.911 (5)	0.811 (26)	0.888 (3)	0.833 (34)
Red-shafted	—	0.929 (4)	0.800 (1)	0.903 (5)
Weighted mean[a]	0.852 (26)	0.826 (42)	0.866 (4)	0.838 (72)

[a] Weighted means for each phenotype averaged over all crosses.

(1984) as an index of winter productivity. Other factors potentially influencing seasonality of resources either did not vary among sites (population density) or do not influence geographic patterns of clutch size in this species (summer AE; Koenig 1984). Thus, we feel that sources of ecological variation in clutch size are as comparable among these sites as possible in any study encompassing a geographical gradient.

One ecological factor, date, had a significant influence on clutch size, with clutch size being significantly lower in late clutches. Koenig (1984) found that clutch size increases with date, whereas there was a highly significant decrease in late clutches sizes at the four live-study sites reported here. The obvious, although not necessarily correct, explanation for this seemingly contradictory result is that Koenig's sample included clutches from a broad range of latitudes; clutches from low latitudes are smaller, and they are also initiated earlier, on average, because breeding commences earlier in the south.

Our goal was to determine whether there is reduced fertility or increased developmental failure in flickers from the Northern Flicker hybrid zone. Evidence of reduced hybrid fitness would suggest that this apparently stable hybrid zone is best explained by a dynamic-equilibrium model. Failure to find this kind of dysgenesis would favor a bounded hybrid-superiority model or some other explanation (Moore 1977). In testing the alternatives, it is important to point out that the hybrid-superiority model refers to ecological or exogenous fitness parameters, whereas the dynamic-equilibrium model requires depression of endogenous fitness parameters in hybrids, i.e. infertility, developmental aberrations, failure to maintain physiological homeostasis, etc. Thus, the bounded hybrid-superiority hypothesis does not predict increased clutch size, etc., but rather a failure to find a reduction in these reproductive parameters in hybrid phenotypes.

If reduced hybrid fitness were a factor maintaining the Northern Flicker hybrid zone, we would expect a reduction in one or more of the three reproductive parameters (clutch size, brood size, or the ratio of the two) at the two central hybrid locales (Bridgeport and Morrill) relative to the two distal locales (Sutherland and Wheatland) and the two museum egg collection samples. This was not the case. Reshuffling the data such that the reproductive parameters were compared across adult phenotypes (Table 3) resulted in one significant test. Specifically, males with hybrid phenotypes seemed to be associated with reduced brood size, but, as discussed in the results, this was an enigmatic result when explained in terms of reduced hybrid fitness. When the data set was reshuffled again, such that developmental success (brood-size/clutch-size) could be compared between different types of cross (Table 4), there were no significant differences. Considering comparisons for clutch size, brood size, and the ratio between the two, 10 statistical tests were performed where reduced hybrid fitness might have manifested. Only one test was significant ($P < 0.04$), and this could be attributed reasonably to chance alone.

Because of limited sample sizes we cannot state conclusively that there is no reduction in hybrid fitness in the Northern Flicker hybrid zone; however, we can state that if it is there, it is very slight. This overall lack of evidence for hybrid unfitness is inconsistent with either the dynamic-equilibrium or the reinforcement model. Of the two remaining alternatives (Moore 1977), the bounded hybrid-superiority model appears the more likely explanation of the Northern Flicker hybrid zone because the hybrid zone is not growing broader, as predicted by the introgression model (Moore and Buchanan 1985).

The Northern Flicker hybrid zone is one of a substantial number of avian hybrid zones (see Short 1969, Moore 1977, and Rising 1983a for reviews). Although few of these have been studied in detail, it is apparent that the flicker hybrid zone is *not* paradigmatic for *all* avian hybrid zones. For example, the hybrid zone between the Blue-winged (*Vermivora pinus*) and Golden-winged (*V. chrysoptera*) warblers has moved substantially in historical times (Gill 1980). Reproductive isolation appears to have evolved in a portion of the Northern Oriole (*Icterus galbula*) hybrid zone (Corbin and Sibley 1977), although major portions of the hybrid zone remain unchanged (Rising 1983b). Johnson and Johnson (1985) described natural hybridization between the Red-breasted (*Sphyrapicus ruber daggetti*) and Red-naped (*S. nuchalis*) sapsuckers. This is presumably an old secondary contact and hybridization persists, but this situation is best described as a zone of overlap and hybridization (Short 1969) because parental phenotypes predominate numerically. The sapsuckers clearly mate assortatively, and Johnson and Johnson (1985) argued from indirect evidence that hybrids assorted from the F_1s were selected against. The Northern Flicker hybrid zone, in contrast, appears stable, and there is no evidence of preferential mating (Moore and Buchanan 1985) or of hybrid breakdown. Furthermore, hybridization is rampant, one infrequently sees a pure Red- or Yellow-shafted Flicker in the center of the hybrid zone, and the zone covers a large geographical area (Short 1965).

A monumental question is whether one type of hybrid zone evolves into another, particularly as a result of selection forces operating within the hybrid zone. This appears to be the case in the Northern Oriole. On the other hand, the flicker hybrid zone must be at least as old, but evolution of reproductive isolation has not progressed there (Moore and Buchanan 1985). Dowling and Moore (1984, 1985) described a zone of overlap and hybridization between the common and the striped shiner (*Notropis*) that is comparable to the sapsucker hybrid zone in a number of respects. Despite the antiquity of that zone and clear evidence for selection against hybrids, reproductive isolation between the shiners is far from complete. This raises the possibility that premating reproductive isolating mechanisms do not evolve in hybrid zones even when the hybrids are selected against. When some measure of premating reproductive isolation (assortative mating) is seen in a hybrid zone, it is possible that it evolved *in situ* as an adaptive response to selection against hybrids. Alternatively, it is possible that its evolution was incidental to the hybrid zone. In the case of the sapsuckers, for example, the red-breasted are known to return to seasonal nesting areas earlier than the red-naped, and this no doubt contributes to the low level of interspecific matings. It is possible that selection has favored early and late migration in the respective species and this, incidentally, has resulted in a reduced level of hybridization in the limited areas of sympatry. Although it is important to recognize these alternatives as a guide to future research, the present data are too few to develop a reasoned inference as to the relationships among different kinds of hybrid zones.

ACKNOWLEDGMENTS

We thank James Haugland of Sutherland, Nebraska; Donald Lindgren of Bridgeport, Nebraska; Sam Masid of Morrill, Nebraska; and Buddy Wilson of Wheatland, Wyoming for allowing us to conduct this research on their property. We thank Thad Grudzien for critically reading the manuscript and Lori Merlotti for helping with the preparation of the manuscript. We thank Ned K. Johnson, Peter G. Connors, and an anonymous reviewer for many thoughtful and useful comments that were incorporated into the revised manuscript. This research was sponsored by NSF grants BSR 81-05195 and BSR 83-20605 to William S. Moore. Compilation of the museum data was made possible by a grant from the Frank M. Chapman Memorial Fund to Walter D. Koenig.

LITERATURE CITED

BARROWCLOUGH, G. F. 1980. Genetic and phenotypic differentiation in a Wood Warbler (genus *Dendroica*) hybrid zone. Auk 97: 655-668.

BARTON, N. H. 1979. The dynamics of hybrid zones. Heredity 43: 341-359.

———, & G. H. HEWITT. 1981. Hybrid zones and speciation. Pp. 109-145 *in* Essays on evolution and speciation in honor of M. J. D. White (W. R. Atchley and D. S. Woodruff, Eds.). Cambridge, England, Cambridge Univ. Press.

BOCK, C. E. 1971. Pairing in hybrid flicker populations in eastern Colorado. Auk 88: 921-924.

CORBIN, K. W., & C. G. SIBLEY. 1977. Rapid evolution in orioles in the genus *Icterus*. Condor 79: 335-342.

DOWLING, T. E., & W. S. MOORE. 1984. Level of reproductive isolation between two cyprinid fishes, *Notropis cornutus* and *N. chrysocephalus*. Copeia 1984: 617–628.

———, & ———. 1985. Evidence for selection against hybrids in the family Cyprinidae (genus *Notropis*). Evolution 39: 152–158.

GILL, F. B. 1980. Historical aspects of hybridization between Blue-winged and Golden-winged warblers. Auk 97: 1–18.

JOHNSON, N. K., & C. B. JOHNSON. 1985. Speciation in sapsuckers (*Sphyrapicus*): II. Sympatry, hybridization, and mate preference in *S. ruber daggetti* and *S. nuchalis*. Auk 102: 1–15.

KOENIG, W. D. 1982. Ecological and social factors affecting hatchability of eggs. Auk 99: 526–536.

———. 1984. Geographic variation in clutch size in the Northern Flicker (*Colaptes auratus*): support for Ashmole's hypothesis. Auk 101: 698–706.

LEHRMAN, D. S. 1965. Interaction between internal and external environments in the regulation of the reproductive cycle of the Ring Dove. Pp. 355–380 *in* Sex and behavior (F. A. Beach, Ed.). New York, John Wiley & Sons.

MOORE, W. S. 1977. An evaluation of narrow hybrid zones in vertebrates. Quart. Rev. Biol. 52: 263–277.

———, & D. B. BUCHANAN. 1985. Stability of the Northern Flicker hybrid zone in historical times: implications for adaptive speciation theory. Evolution 39: 135–151.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, & D. H. BENT. 1975. SPSS, statistical package for the social sciences, 2nd ed. New York, McGraw-Hill.

REMINGTON, C. L. 1968. Suture-zones of hybrid interaction between recently joined biotas. Pp. 321–428 *in* Evolutionary biology, vol. 2 (T. Dobzhansky, M. K. Hecht, and W. C. Steere, Eds.). New York, Appleton-Century-Crofts.

RICKLEFS, R. E. 1980. Geographic variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97: 38–49.

RISING, J. D. 1983a. The Great Plains hybrid zones. Pp. 131–157 *in* Current ornithology, vol. 1 (R. F. Johnston, Ed.). New York, Plenum Publ. Corp.

———. 1983b. The progress of oriole hybridization in Kansas, USA. Auk 100: 885–897.

SHERMAN, A. R. 1910. At the sign of the Northern Flicker. Wilson Bull. 22: 133–171.

SHORT, L. L. 1965. Hybridization in the flickers (*Colaptes*) of North America. Bull. Amer. Mus. Nat. Hist. 129: 307–428.

———. 1969. Taxonomic aspects of avian hybridization. Auk 86: 84–105.

———. 1970. A reply to Uzzell and Ashmole. Syst. Zool. 19: 199–201.

THORNTHWAITE ASSOCIATES. 1964. Average climatic water balance data of the continents, part VII. Lab. Climatol. Publ. Climatol. 17: 419–615.

WILSON, E. O. 1965. The challenge from related species. Pp. 7–25 *in* The genetics of colonizing species (H. G. Baker and G. L. Stebbins, Eds.). New York, Academic Press.

The American Ornithologists' Union solicits nominations for its **Brewster and Coues Awards.** Nominations and supporting materials should be sent to **Dr. Elsie C. Collias, Department of Biology, University of California, Los Angeles, California 90024.** Materials must be received before **1 March 1986.**

Wisconsin Project Loon Watch is accepting applications for its first annual **Sigurd T. Olson Common Loon Research Award** for research on Common Loons in the Lake Superior-Lake Michigan region of the United States and Canada. To apply, submit a brief (maximum 10 pages) description of the proposed research program and curriculum vitae to **Dr. Paul I. V. Strong, Director, Wisconsin Project Loon Watch, Sigurd Olson Environmental Institute, Northland College, Ashland, Wisconsin 54806 USA** no later than **1 March 1986.** Proposals by students should be accompanied by two letters of recommendation. The $1,000 award will be granted on the basis of the project's potential to better understand and manage Upper Great Lakes populations of Common Loons.

BROOD PARASITISM IN A HOST GENERALIST, THE SHINY COWBIRD:
I. THE QUALITY OF DIFFERENT SPECIES AS HOSTS

PAUL MASON[1]

Department of Zoology, University of Texas, Austin, Texas 78712 USA

ABSTRACT.—The Shiny Cowbird (*Molothrus bonariensis*) of South America, Panama, and the West Indies is an obligate brood parasite known to have used 176 species of birds as hosts. This study documents wide variability in the quality of real and potential hosts in terms of response to eggs, nestling diet, and nest survivorship. The eggs of the parasite are either spotted or immaculate in eastern Argentina and neighboring parts of Uruguay and Brazil. Most species accept both morphs of cowbird eggs, two reject both morphs, and one (Chalk-browed Mockingbird, *Mimus saturninus*) rejects immaculate eggs but accepts spotted ones. No species, via its rejection behavior, protects the Shiny Cowbird from competition with a potential competitor, the sympatric Screaming Cowbird (*M. rufoaxillaris*). Cross-fostering experiments and natural-history observations indicate that nestling cowbirds require a diet composed of animal protein. Because most passerines provide their nestlings with such food, host selection is little restricted by diet. Species-specific nest survivorship, adjusted to appropriate values of Shiny Cowbird life-history variables, varied by over an order of magnitude. Shiny Cowbirds peck host eggs. This density-dependent source of mortality lowers the survivorship of nests of preferred hosts and creates natural selection for greater generalization. Host quality is sensitive to the natural-history attributes of each host species and to the behavior of cowbirds at nests. *Received 4 June 1984, accepted 26 June 1985.*

VARIATION in resource quality can have great ecological and evolutionary consequences. Obligate brood parasites never build nests but leave the care of their eggs and young to other species, their hosts. The parental behavior of hosts is a critical and quantifiable resource to brood parasites. The first task in understanding the use of resources is to ascertain the quality of each alternative. I surveyed the quality of various passerine species as hosts of the Shiny Cowbird (*Molothrus bonariensis*) in Buenos Aires Province, Argentina. Host quality is tractable to analysis because selection is spatially and temporally focused at nests. Dimensions of host quality examined include response to parasitic eggs, nestling diet, and characteristic survivorship of each species' nests. This is the only systematic attempt to characterize the quality of an array of species for any brood parasite.

The Shiny Cowbird is widely distributed throughout South America (Friedmann 1929). It is an extreme host generalist, known to have parasitized 176 species (Friedmann et al. 1977). The Shiny Cowbird is sympatric with a potential competitor, the Screaming Cowbird (*M. rufoaxillaris*), in Argentina, Uruguay, and neighboring parts of South America. This latter species is extremely specialized on the cooperatively nesting Bay-winged Cowbird (*M. badius*), although anecdotal reports of its use of other hosts exist (Hudson 1874, 1920; Grant 1911, 1912; Pereyra 1938; Hoy and Ottow 1964).

Experiments that simulate natural parasitism provide two kinds of important information. First, the technique identifies individuals that reject parasitic eggs. This response is apparently species typical for North American birds (Rothstein 1975a, b). Rejecter species can easily be regarded as unsuitable to cowbirds on the basis of this single criterion (Rothstein 1982). Second, if a species is an accepter, then observed parasitism accurately reflects use of that species. If both Shiny Cowbird and Screaming Cowbird eggs appear in nests, the two parasitic species are potentially in competition. Experiments in artificial parasitism can reveal if certain species reject eggs of one species but accept those of the other.

Categorization of species as accepters or re-

---

[1] Present address: Department of Biological Sciences, University of California, Santa Barbara, California 93106 USA.

jecters is complicated by extreme variation in Shiny Cowbird eggs. Some species may reject one egg type but accept many others. Despite the unusual level of variation, two broad classes of eggs are recognized: spotted and immaculate (Friedmann 1929, Fraga 1978, Gochfeld 1979). More importantly, I found no evidence that birds discriminated against eggs within each category, and this is the primary justification for the dichotomous categorization (see Results). Screaming Cowbird eggs (described in detail by Fraga 1983a) are spotted, but the maculations are less distinct. Most also possess miniscule scrawls.

Nestling diet is another critical aspect of host quality. Cross-fostering, the introduction of parasitic young into nests, is a difficult but informative technique capable of assessing host dietary quality. Failing this, descriptions of food items brought to nests may be adequate.

Nests are subject to total failure for reasons such as predation and severe weather. Survivorship estimates are appropriate measures of this aspect of host quality.

METHODS

Observations were carried out almost daily for two seasons (1977–1978 and 1978–1979) at two sites 17.6 km apart near Magdalena, Buenos Aires Province, Argentina. Descriptions of the study sites, the avifauna, and my general field techniques appear elsewhere (Mason 1985). The habitat consisted of pasture, with clumps of trees and marsh. I searched continually for nests to carry out manipulations and make observations. Of course, nests that were difficult to find or examine are underrepresented in the sample.

The technique of artificial parasitism followed Rothstein (1971), except that I occasionally placed 2 eggs in a single nest. The experiments used real and artificial eggs of 3 experimental morphs: spotted *M. bonariensis*, white *M. bonariensis*, and *M. rufoaxillaris*. Dimensions and weights of real and artificial eggs can be found in Mason (1980). Experimental parasitism was performed as early as possible, and always before 1200. This corresponds to the natural laying behavior of Shiny Cowbird females (Hoy and Ottow 1964).

There are two mutually exclusive responses to parasitic eggs: acceptance for incubation, or rejection. Rejection includes any behavior of the host species that does not result in successful incubation: ejection of the parasitic egg, nest desertion, or burial of the parasitic egg. I scored an experimentally placed egg as accepted if it remained in the nest 5 days or more (see Rothstein 1975a). Large series of experiments with North American bird species indicate that almost all rejections occur within this period (Rothstein 1975a, Mason unpubl. data).

Species were categorized as accepters or rejecters for specific egg types if two-thirds or more of the responses were consistent. Usually, responses are more consistent, but Rothstein (1975b) used this truncation criterion to show that species' responses were distributed bimodally. Species were not categorized if the frequency of rejection fell between one-third and two-thirds. Species were tentatively regarded as accepters of any egg morph with which they were not tested if (1) the species clearly accepted cowbird eggs widely divergent from its own eggs; or (2) the untested morph closely resembled its own. For example, a species laying an immaculate white egg and shown experimentally to accept spotted eggs would be tentatively categorized as an accepter of immaculate cowbird eggs.

To assess dietary quality and response to nestlings, I augmented observations of nestling development with cross-fostering experiments. If a nestling cowbird remained healthy on subsequent visual inspections, dietary quality was scored as acceptable. Unhealthy birds were recognized by any of the following symptoms: pallor, emaciation, loss of thermoregulatory ability, or moribund passivity. Ideally, cross-fostered cowbirds should be larger than host young to eliminate the possibility that subsequent starvation of the cowbird is the result of a competitive disadvantage and not of dietary quality.

Host species were scored as acceptable with respect to diet if cross-fostered nestlings fledged. If nestlings appeared healthy before nest failure (occurring for reasons unrelated to parasitism), the host was scored as tentatively acceptable.

Nest survivorship can estimate the parasite's expectation of success, provided the host fulfills the other requirements for acceptability. I measured the probability of survival for the egg and nestling phases, considering only those sources of mortality that affected all nest occupants similarly and simultaneously. Survivorship of each interval was calculated by raising daily survivorship to a power equal to the length of that interval in days (Mayfield 1975, Hensler and Nichols 1981). Because cowbirds differ from most of their hosts in length of the incubation and nestling periods, I used the appropriate values of these Shiny Cowbird life-history variables (11.9 days and 13.9 days, respectively; Mason unpubl. data) to find the specific value of the host to cowbirds. The length of the egg phase includes the laying period of the host as well as the incubation period of the cowbird egg. Survivorship to fledging is the product of survivorship during the egg and the nestling phases. The survivorship estimates reflect freedom of the nest

TABLE 1. Passerine response to cowbird eggs. Experimental eggs were of 3 morphs: immaculate Shiny Cowbird (Shiny, I), spotted Shiny Cowbird (Shiny, S), and Screaming Cowbird (Screaming).

	Response to experimental egg morphs[a]		
	Shiny, I	Shiny, S	Screaming
Host species[b]	R/T (Status)	R/T (Status)	R/T (Status)
Rufous Hornero, *Furnarius rufus* (I)	4/5 (Rej)	5/6 (Rej)	4/4 (Rej)
Wren-like Rushbird, *Phleocryptes melanops* (I)	0/5 (Acc)	0/7 (Acc)	0/4 (Acc)
Tufted Tit-Spinetail, *Leptasthenura platensis* (I)	0/1 (Acc)	0/4 (Acc)	0/2 (Acc)
Little Thornbird, *Phacellodomus sibilatrix* (I)	— (Acc?)[c]	0/1 (Acc)	— (Acc?)
Freckle-breasted Thornbird, *Phacellodomus striaticollis* (I)	— (Acc?)	0/1 (Acc)	0/2 (Acc)
Firewood-gatherer, *Anumbius annumbi* (I)	— (Acc?)	0/6 (Acc)	0/4 (Acc)
Vermillion Flycatcher, *Pryocephalus rubinus* (S)	0/6 (Acc)	0/6 (Acc)	0/3 (Acc)
Yellow-browed Tyrant, *Satrapa icterophrys* (S)	1*/3[d] (Acc)	0/2 (Acc)	0/1 (Acc)
Cattle Tyrant, *Machetornis rixosus* (S)	0/2 (Acc)	— (Acc?)	— (Acc?)
Fork-tailed Flycatcher, *Tyrannus savana* (S)	3/3 (Rej)	2/2 (Rej)	— (Rej?)
Great Kiskadee, *Pitangus sulphuratus* (S)	0/4 (Acc)	1/2 ?	1/2 ?
White-crested Tyrannulet, *Serpophaga subcristata* (I)	— (Acc?)	0/1 (Acc)	0/1 (Acc)
House Wren, *Troglodytes aedon* (S)	0/3 (Acc)	— (Acc?)	— (Acc?)
White-rumped Swallow, *Tachycineta leucorrhoa* (I)	— (Acc?)	0/3 (Acc)	0/1 (Acc)
Brown-chested Martin, *Phaeoprogne tapera* (I)	— (Acc?)	0/1 (Acc)	— (Acc?)
Chalk-browed Mockingbird, *Mimus saturninus* (S)	8*/11 (Rej)	2*/10 (Acc)	6/12 ?
Creamy-bellied Thrush, *Turdus amaurochalinus* (S)	0/1 (Acc)	— (Acc?)	— (Acc?)
Masked Gnatcatcher, *Polioptila dumicola* (S)	0/1 (Acc)	— (Acc?)	— (Acc?)
Bay-winged Cowbird, *Molothrus badius* (S)	0/6 (Acc)	— (Acc?)	0/1 (Acc)
Blue-and-yellow Tanager, *Thraupis bonariensis* (S)	0/1 (Acc)	— (Acc?)	0/1 (Acc)
Saffron Finch, *Sicalis flaveola* (S)	0/4 (Acc)	0/8 (Acc)	2**/8 (Acc)
Grassland Yellow-Finch, *Sicalis luteola* (S)	0/2 (Acc)	— (Acc?)	— (Acc?)
Grassland Sparrow, *Ammodramus humeralis* (S)	0/1 (Acc)	— (Acc?)	— (Acc?)
Rufous-collared Sparrow, *Zonotrichia capensis* (S)	2**/6 (Acc)	1*/5 (Acc)	0/7 (Acc)
Hooded Siskin, *Carduelis magellanica* (S or I)	— ?	0/1 (Acc)	0/1 (Acc)
House Sparrow, *Passer domesticus* (S)	0/1 (Acc)	0/1 (Acc)	— (Acc?)

[a] R/T represents the number of rejections out of the number of trials. Acc = accepts, Rej = rejects.

[b] Common names according to Meyer de Schauensee (1970). The letter in parentheses following each species name roughly categorizes the eggs of that species as spotted (S) or immaculate (I). More detailed descriptions of eggs are in Mason (1985).

[c] Species that accepted eggs widely divergent from their own, but untested for morphs more similar to their own, are tentatively scored as accepters, as indicated by a question mark.

[d] Each asterisk indicates a case of desertion.

from complete loss, but do not include events that cause differential mortality within the nest.

Scientific names of species are given in Table 1.

RESULTS

Responses to eggs.—I performed 187 experimental egg manipulations and scored 42 responses as rejections. Species could almost always be categorized as accepters or rejecters, although only for a specific egg morph in the case of the Chalk-browed Mockingbird (Table 1). Species classified as rejecters of all eggs (Rufous Hornero, Fork-tailed Flycatcher) may be referred to as dual rejecters, and those classified as accepters of all as dual accepters. The Chalk-browed Mockingbird is a differential accepter, favoring the spotted Shiny Cowbird egg morph. Two species, the Chalk-browed Mockingbird and the Great Kiskadee, showed intermediate levels of ejection for certain morphs. In the case of the kiskadee, the problem may be one of small sample sizes (4 experiments with spotted eggs), but this is not true for the mockingbird, which rejected Screaming Cowbird eggs from 6 of 12 nests. I have not assigned rejecter or accepter status to either species.

Eight rejections occurred by desertion and none by egg burial. Unlike ejection, desertion was never expressed consistently. No species could be classified as a rejecter on the basis of desertion.

No evidence suggests that response to artificial eggs differs from response to natural eggs. To use the Chalk-browed Mockingbird as an example, responses to real and artificial eggs

TABLE 2. Results of cross-fostering experiments. Number of experiments for each host species is indicated in parentheses. See text for discussion.

Host species	Results
Rufous Hornero (1)	4-day-old nestling lived 4 more days before starvation, losing in competition with much bigger host nestlings
Firewood-gatherer (1)	Lived 3–4 days before death of all nestlings due to botfly parasitism
Vermillion Flycatcher (1)	Lived 2–3 days until predation
Yellow-browed Tyrant (1)	Lived 5 days until predation
Great Kiskadee (1)	Nestling of several days fledged after 9 more days in nest
Chalk-browed Mockingbird (2)	Nestling at first nest lived 4–5 days until predation at nest; nestling at second nest lived 6–7 days until predation at nest
Creamy-bellied Thrush (1)	Fledged after 14–15 days in nest, but at very low weight, having hatched 4 days after host nestling
Saffron Finch (2)	Nestling Shiny Cowbird lived 2 days until death of all nestlings due to botfly parasitism; nestling Screaming Cowbird failed within 2 days
House Sparrow (1)	Failed within 2 days

were statistically indistinguishable ($P > 0.5$ for all comparisons among immaculate and spotted Shiny Cowbird eggs and Screaming Cowbird eggs; Fisher's exact test, Siegel 1956). Furthermore, the assignment of species as accepters or rejecters (Table 1) agrees with Fraga (1978, 1980, 1983b, 1985) for 11 common species, including all rejecters. Observations of natural parasitism agree (Mason 1986).

Lack of competition from the Screaming Cowbird.—In all but one case (Chalk-browed Mockingbird), birds responded to Screaming Cowbird eggs as they did to spotted Shiny Cowbird eggs. No host species totally protects the Shiny Cowbird from competition with the Screaming Cowbird via its rejection behavior. Since Screaming Cowbird eggs were found only in nests of the Bay-winged Cowbird (Mason 1980), host selection in the Shiny Cowbird is unaffected by nestling competition with the former species in all other nests.

Nestling diet.—I performed 11 cross-fostering experiments (Table 2). Only 2 species were scored as having unacceptable diets: the Saffron Finch and the House Sparrow. Observations of natural parasitism support the experiments in the case of the finch: 2 Shiny Cowbirds in separate nests both failed to survive 2 days. No fledging records exist for either species. The remaining species were judged as acceptable, and observations support this interpretation. Differential mortality of the cowbird nestling occurred at 1 nest of the Rufous Hornero, and 1 nest of the Creamy-bellied Thrush. Both deaths were attributed to intranest competition because host young had a substantial size advantage (Table 2). The hornero has been known to rear cowbirds in other areas of South America (Friedmann 1929, Friedmann et al. 1977, Salvador 1983). A second thrush nest was found with 2 cowbirds about to fledge. The experimental nestling (in the thrush nest) weighed 22.0 g at fledging, while the 2 nestlings at the other nest weighed 43.0 and 45.5 g.

Dietary suitability (Table 3) was judged by 3 criteria: species reported to successfully rear naturally placed eggs (Friedmann 1929, 1963; Friedmann et al. 1977; Fraga 1978; this study), species that feed young animal protein (Mason 1985), and the results of the cross-fostering experiments.

Nest survivorship.—Complete data on daily survivorship are in Mason (1985). Daily survivorship for the egg phase ranged from 0.988 (Rufous Hornero, $n = 15$ nests, 244 days of observation) to 0.852 (White-crested Tyrannulet, $n = 4$ nests, 27 days of observation). Daily survivorship for the nestling phase ranged from 0.996 (Rufous Hornero, $n = 13$ nests, 285 days of observation) to 0.857 (Fork-tailed Flycatcher, $n = 4$ nests, 28 days of observation).

The hornero's superior survivorship for both phases of the nesting cycle is largely attributable to its remarkable domed mud nest, which contributes to superior survivorship in other birds that also use it (Mason 1985). The difference between survivorship in hornero and mockingbird nests was significant for both phases of the nesting cycle (Table 4). Mockingbird survivorship exceeded that of the Rufous-

TABLE 3. Dietary suitability of different host species. Descriptions of food items can be found in Mason (1985). Cross-fostering experiments are discussed in Table 2 and text.

Host species	Natural successful rearing?	Animal protein provided?	Successful cross-fostering?
Rufous Hornero	Yes[a]	Yes	Yes?
Wren-like Rushbird		Yes	
Freckle-breasted Thornbird		Yes	
Firewood-gatherer	Yes[a]		Yes
Vermillion Flycatcher		Yes	Yes
Yellow-browed Tyrant	Yes[b]	Yes	Yes
Cattle Tyrant	Yes[a]		
Fork-tailed Flycatcher	Yes[a]		
Tropical Kingbird (*Tyrannus melancholicus*)	Yes[a]		
Great Kiskadee		Yes	Yes
White-rumped Swallow	Yes[b]		
House Wren	Yes[a,b]		
Chalk-browed Mockingbird	Yes[a,b]	Yes	
Rufous-bellied Thrush (*Turdus rufiventris*)	Yes[a,b]		
Creamy-bellied Thrush	Yes[b]		Yes?
Masked Gnatcatcher	Yes[a]		
Bay-winged Cowbird	Yes[a]	Yes	
Yellow-winged Blackbird (*Agelaius thilius*)	Yes[b]		
Blue-and-yellow Tanager	Yes[a]		
Saffron Finch	No[b]	No	No?
Grassland Yellow-Finch	No[a]	No	
Rufous-collared Sparrow	Yes[a,b]	Yes	
Hooded Siskin	Yes[a]		
House Sparrow	No[a]	Variable	No

[a] Records from literature (Friedmann 1929, 1963; Friedmann et al. 1977; Salvador 1983; Fraga 1985).

[b] Observations of this study.

collared Sparrow only for the nestling phase when all sources of mortality were considered. However, 13 mockingbird nest failures were attributed to pecking by Shiny Cowbirds, while only 1 such loss occurred at sparrow nests, and none occurred at nests of the hornero. When this source of mortality was removed, the daily survivorship of mockingbird nests improved significantly, surpassing that of the sparrow but remaining inferior to that of the hornero.

The product of the survivorship probabilities for the egg and nestling phases represents the probability of a nest fledging at least one young Shiny Cowbird under ideal conditions. The accepter species differed by almost an order of magnitude; when rejecters were considered, the difference was greater still (Table 5). Rejecters are included to show the success a female could experience were she to lay a mimetic egg. The Rufous Hornero, in the absence of rejection behavior, would be the best host choice. The best accepter species judged by survivorship (White-rumped Swallow) tended Shiny Cowbird fledgings more frequently than any other species (Table 6; Mason 1986).

DISCUSSION

Response to eggs.—The 26 species surveyed responded to 3 particular morphs of cowbird eggs in a species-typical fashion, with only 2 minor exceptions. This agrees with data from North America (Rothstein 1975a, b). In further agreement, rejection is almost always accomplished by ejection of the parasitic egg. Two species were classified as dual rejecters (Rufous Hornero, Fork-tailed Flycatcher) and one as a differential accepter favoring the spotted morph (Chalk-browed Mockingbird). Species that reject cowbird eggs are obviously unsuitable as hosts.

Desertion was infrequent, and egg burial was never observed. This also resembles most North American experiments in artificial parasitism

TABLE 4. Comparisons of daily mean survivorship rates. Numbers are presented as daily survivorship (SD, no. of nests surveyed, no. of observation days).

			z	F (z)	P
	Rufous Hornero vs. Chalk-browed Mockingbird				
Eggs	0.988 (0.007, 15, 244)	0.922 (0.012, 59, 477)	4.75	0.999+	<0.001, 1-tailed
Eggs[a]	0.988 (0.007, 15, 244)	0.950 (0.010, 59, 477)	3.11	0.999	=0.001, 1-tailed
Nestlings	0.996 (0.004, 13, 285)	0.953 (0.014, 28, 235)	2.95	0.998	=0.002, 1-tailed
	Chalk-browed Mockingbird vs. Chalk-browed Mockingbird[a]				
Eggs	0.922 (0.012, 59, 477)	0.950 (0.010, 59, 477)	1.79	0.963	=0.037, 1-tailed
	Chalk-browed Mockingbird vs. Rufous-collared Sparrow				
Eggs	0.922 (0.012, 59, 477)	0.899 (0.020, 45, 227)	0.99	0.839	=0.161, NS
Eggs[a]	0.950 (0.010, 59, 477)	0.903 (0.020, 45, 227)	2.10	0.982	=0.018, 1-tailed
Nestlings	0.953 (0.014, 28, 235)	0.901 (0.024, 26, 161)	1.87	0.969	=0.031, 1-tailed

[a] Nest failures due to pecking of eggs by Shiny Cowbirds eliminated from calculation of survivorship.

(Rothstein 1975a, b; but see Clark and Robertson 1981). Desertion may be a response to human presence or some disturbance at the nest other than the parasitic egg (Rothstein 1975a, 1976), but my techniques could not identify this possibility.

The species most likely to desert was the Rufous-collared Sparrow, which rejected only 3 of 18 artificially placed cowbird eggs, all by desertion. Fraga (1978) also found desertion to be infrequent. Hudson (1920) claimed that desertion was the typical response to parasitism in the Vermillion Flycatcher, but I observed acceptances in all 19 experiments.

Cowbird eggs incubated in nests of differential accepters fulfill the biological criterion for mimicry. Their resemblance to host eggs is adaptive and subject to selection. Human standards of similarity are misleading and inappropriate. For example, Chalk-browed Mockingbird eggs are easily distinguished (by humans) from spotted Shiny Cowbird eggs that are readily accepted. Three additional species are suspected of being differential accepters (Fraga 1985).

Nestling diet.—Cowbirds appear to require animal protein. Because most passerines feed their young arthropods (Hamilton and Orians 1965, Skutch 1976) and measures of overlap in nestling diets of sympatric species are typically high (Orians and Horn 1969, Anderson 1978, Maher 1979), cowbirds are probably little restricted in host choice by factors associated with nestling nutrition. This claim is supported by the large and taxonomically diverse list of species known to have reared Brown-headed (*M. ater*), Bronzed (*M. aeneus*), and Shiny cowbirds (Post and Wiley 1976, 1977; Friedmann et al. 1977).

Only 3 species (Saffron Finch, Grassland Yellow-Finch, Hooded Siskin) at my study sites are seed specialists. Neither finch is known to have reared cowbirds to fledging (Friedmann et al. 1977). Shiny Cowbird deaths in nests of the Grassland Yellow-Finch have been attributed to diet (Salvador 1983, Fraga 1985). Other seed specialists (*Carduelis* spp.) may augment the nestling diet with aphids, although reports are variable (Bent and collaborators 1968, Friedmann et al. 1977). Friedmann et al. (1977: 43) and Middleton (1977) observed Brown-headed Cowbirds to die in goldfinch nests.

The failure of a cross-fostered cowbird to survive in a nest of the House Sparrow is consistent with observations by Salvador (1983) and the lack of fledging records (Friedmann et al. 1977). Because seeds often form a substantial portion of the nestling diet, failures are probably due to dietary restriction rather than to discrimination against young cowbirds (Barrows 1889, Seel 1969, Anderson 1978, Eastzer et al. 1980).

Nest survivorship.—One source of nest failure was pecking by Shiny Cowbirds. Nests of highly preferred hosts are often multiply parasitized by several females (Fraga 1985; Mason 1980, 1986) and consequently subject to higher levels of pecking. This behavior depressed the success of Chalk-browed Mockingbird nests to a level not significantly different from that of the Rufous-collared Sparrow (Table 4). Pecking is sometimes less drastic, and cowbird eggs are occasionally lost during otherwise successful nesting attempts. Nonetheless, losses to peck-

TABLE 5. Survivorship estimates of Shiny Cowbirds in nests of different host species. Species with unsuitable nestling diets are not included.

	Survivorship		
	Eggs	Nestlings	Overall[a]
Rufous Hornero[b]	0.823 (15, 244)[c]	0.952 (13, 285)	0.783
Wren-like Rushbird	0.596 (20, 271)	0.715 (11, 126)	0.426
Tufted Tit-Spinetail	0.306 (4, 25)	1.000 (2, 31)	0.306
Freckle-breasted Thornbird	0.211 (7, 60)	0.746 (4, 48)	0.157
Firewood-gatherer	0.607 (11, 120)	0.671 (8, 106)	0.407
Vermillion Flycatcher	0.403 (22, 151)	0.405 (14, 143)	0.163
Yellow-browed Tyrant	0.713 (10, 95)	0.486 (8, 79)	0.347
Fork-tailed Flycatcher[b]	0.549 (7, 72)	0.117 (4, 28)	0.064
Great Kiskadee[d]	0.489 (7, 106)	0.481 (3, 39)	0.235
White-rumped Swallow	0.584 (9, 89)	0.819 (5, 70)	0.478
House Wren	0.273 (9, 44)	0.624 (3, 41)	0.170
Chalk-browed Mockingbird[e]	0.326 (59, 477)	0.514 (28, 235)	0.168
Rufous-bellied Thrush	0.370 (3, 30)	0.408 (2, 16)	0.151
Bay-winged Cowbird	0.190 (10, 82)	1.000 (2, 20)	0.190
Rufous-collared Sparrow	0.227 (45, 227)	0.233 (26, 161)	0.053

[a] Overall survivorship = (egg survivorship) × (nestling survivorship).

[b] Rejects cowbird eggs.

[c] Mean survivorship (no. of nests surveyed, no. of observation days).

[d] Response to spotted eggs uncertain (Mason 1986).

[e] Rejects immaculate cowbird eggs.

ing are density-dependent forms of mortality because they are inflicted by cowbirds

The survivorship probabilities (Table 5) represent the freedom of nests from complete loss, and estimate the success of cowbirds under ideal circumstances. Differential mortality of cowbirds within a nest will lower success below rated survivorship. Competition among nestlings for the limited food available can introduce differential mortality as in adaptive brood reduction (Lack 1954): competition is size and age mediated, and inequalities in competitive ability are introduced by the amount of food supplied, size at hatching, magnitude of hatching asynchrony, and normal nestling growth rate.

Successful parasitism requires that female cowbirds properly synchronize their laying with that of the host. Eggs laid late may fail to hatch, or hatch so late that the nestling will be competitively inferior. The extremely low fledging weight of the cowbird nestling in the nest of the Creamy-bellied Thrush and the death of the cowbird nestling cross-fostered in a nest of the Rufous Hornero are illustrative (Table 2).

The life-history characteristics of some species suggest that severe nestling competition may be difficult to avoid. The advantage of the cowbird's shorter incubation period is offset by the Chalk-browed Mockingbird's larger size at hatching and faster growth rate (Fraga 1985, Mason 1985). I observed only 1 case of starvation among 16 cowbird nestlings in 10 broods, but Fraga (1985) reported 12 such cases among 20 nestlings from 15 nests. The reasons for increased starvation at Fraga's site are unknown.

Competition between host and parasite is unlikely to adversely affect cowbirds in nests of the Rufous-collared Sparrow. Nestling sparrows are smaller at hatching and grow more slowly (King 1973, Fraga 1978, Mason 1985). Fraga (1985) found that the overall success of naturally laid cowbird eggs in Rufous-collared Sparrow nests was 0.056 (vs. 0.053 in Table 4). On the other hand, competition is likely if sparrow nests are multiply parasitized. The nutritional demands of two cowbird young probably exceed the capabilities of that host to rear two healthy cowbirds. Fraga (1978, 1983b, 1985) reported no cases of sparrows fledging two cowbirds, while King (1973) showed that growth rate and fledging weight were both reduced when two cowbird nestlings were in the nest. In the region of South America studied, multiple parasitism is almost entirely restricted to large, highly preferred hosts; smaller hosts (like the sparrow) are slightly used (Mason 1986).

Friedmann (1963) pointed out that the suc-

TABLE 6. Observations of host species attending Shiny Cowbird fledglings.

Host species	Date of observation
White-rumped Swallow (7 nests)	
1	14 Nov 1978, 18 Nov 1978
2	24 Nov 1978, 30 Nov 1978
3	27 Nov 1978, 28 Nov 1978
4	8 Dec 1978, 12 Dec 1978
5	9 Dec 1978, 14 Dec 1978
6	19 Dec 1978
7	23 Dec 1978
House Wren	22 Nov 1978
Yellow-winged Blackbird	12 Jan 1979
Masked Gnatcatcher	2 Feb 1979

cess of cowbirds is characteristically less than that of their hosts. Three important sources of mortality (diet, density-dependent egg pecking, and the adverse affect of intranest competition) are probably the main reasons for this observation.

Host quality is sensitive to the natural-history attributes of nesting species and to cowbird behavior. Some adaptations of cowbirds can circumvent apparent barriers to successful parasitism. Egg rejection can be overcome by mimicry, as has been documented for the Chalk-browed Mockingbird (Fraga 1985, this study). The Rufous Hornero is apparently a frequent host in other parts of Argentina (Friedmann 1929, Friedmann et al. 1977, Salvador 1983), despite its status as a rejecter in Buenos Aires Province. In the case of large hosts, the shorter the host incubation period, the more likely cowbird nestlings will experience severe competition. Egg pecking may reduce nestling competition by selectively destroying host eggs, whose numbers vary inversely with those of the cowbird in Chalk-browed Mockingbird nests (Mason 1980, Fraga 1985). However, entire clutches are often destroyed, thus increasing the relative value of other species. A generalized pattern of resource use results from the Shiny Cowbird's ability to exploit several avenues of adaptive niche expansion.

ACKNOWLEDGMENTS

My fieldwork in Argentina was made possible by the kind help and cooperation of a number of people and agencies. M. Christie first took me into the field in Argentina. I spent my first season with the Earnshaw family (Estancia San Isidro), and my second with A. Landa (Estancia El Talar). The staff of the Museo Argentino de Ciencias Naturales gave me considerable help and encouragement. In particular, I thank J. M. Gallardo (Director), J. R. Navas (Jefe, División de Ornitología), and M. Canevari. R. M. Fraga and S. I. Rothstein have been sources of intellectual stimulation and encouragement. They, L. F. Kiff, V. Nolan, Jr., R. Robertson, S. S. Sweet, and an anonymous reviewer kindly read and commented on earlier versions of the manuscript. Financial support was in part provided by the Frank M. Chapman Fund of the American Museum of Natural History, New York. I was supported by NSF grant BSR 8214999 to S. I. Rothstein during the preparation of the final draft of this paper.

LITERATURE CITED

ANDERSON, T. R. 1978. Population studies of European sparrows in North America. Occ. Pap. Mus. Nat. Hist. Kansas 70: 1–58.

BARROWS, W. B. 1889. The English Sparrow (*Passer domesticus*) in North America, especially in relations to agriculture. U.S. Dept. Agr. Bull. 1: 1–405.

BENT, A. C., & COLLABORATORS. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies, part 1 (O. L. Austin, Ed.). New York, Dover Publ.

CLARK, K. L., & R. J. ROBERTSON. 1981. Cowbird parasitism and the evolution of anti-parasite strategies in the Yellow Warbler. Wilson Bull. 93: 249–258.

EASTZER, D., P. R. CHU, & A. P. KING. 1980. The young cowbird: average or optimal nestling? Condor 82: 417–425.

FRAGA, R. M. 1978. The Rufous-collared Sparrow as a host of the Shiny Cowbird. Wilson Bull. 90: 271–284.

———. 1980. The breeding of Rufous Horneros (*Furnarius rufus*). Condor 82: 58–68.

———. 1983a. The eggs of the parasitic Screaming Cowbird (*Molothrus rufoaxillaris*) and its host, the Bay-winged Cowbird (*M. badius*): is there evidence for mimicry? J. Ornithol. 124: 187–193.

———. 1983b. Parasitismo de cría del renegrido (*Molothrus bonariensis*) sobre el chingolo (*Zonotrichia capensis*): nuevas observaciones y conclusiones. Hornero 12, No. Extraord.: 245–255.

———. 1985. Host-parasite interactions between Chalk-browed Mockingbirds and Shiny Cowbirds. Pp. 829–844 *in* Neotropical ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithol. Monogr. No. 36.

FRIEDMANN, H. 1929. The cowbirds: a study in the biology of social parasitism. Baltimore, C. C. Thomas.

———. 1963. Host relations of the parasitic cowbirds. U.S. Natl. Mus. Bull. 233: 1–276.

———, L. F. KIFF, & S. I. ROTHSTEIN. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contrib. Zool. 235: 1-75.

GOCHFELD, M. 1979. Brood parasite and host coevolution: interactions between Shiny Cowbirds and two species of meadowlarks. Amer. Natur. 113: 865-870.

GRANT, C. H. B. 1911. List of birds collected in Argentina, Paraguay, Bolivia, and southern Brazil, with field notes. Part I, Passeres. Ibis 5, 9th Ser.: 104-131.

———. 1912. Notes on some South American birds. Ibis 1, 10th Ser.: 273-280.

HAMILTON, W. J., III, & G. H. ORIANS. 1965. Evolution of brood parasitism in altricial birds. Condor 67: 361-382.

HENSLER, G. L., & J. D. NICHOLS. 1981. The Mayfield method of estimating nesting success: a model, estimators, and simulation results. Wilson Bull. 93: 42-53.

HOY, G., & J. OTTOW. 1964. Biological and oological studies of the molothrine cowbirds (Icteridae) of Argentina. Auk 81: 186-203.

HUDSON, W. H. 1874. Notes on the procreant instincts of the three species of *Molothrus* found in Buenos Ayres. Proc. Zool. Soc. London: 153-174.

———. 1920. Birds of La Plata, vol. 1. New York, E. P. Dutton.

KING, J. R. 1973. Reproductive relationships of the Rufous-collared Sparrow and the Shiny Cowbird. Auk 90: 19-34.

LACK, D. 1954. The natural regulation of animal numbers. Oxford, Clarendon Press.

MAHER, W. J. 1979. Nestling diets of prairie passerine birds at Matador, Saskatchewan, Canada. Ibis 121: 437-452.

MASON, P. 1980. Ecological and evolutionary aspects of host selection in cowbirds. Unpublished Ph.D. dissertation, Austin, Texas, Univ. Texas.

———. 1985. The nesting biology of some passerines of Buenos Aires, Argentina. Pp. 954-972 *in* Neotropical ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithol. Monogr. No. 36.

———. 1986. Brood parasitism in a host generalist, the Shiny Cowbird: II. Host selection. Auk 103: 61-69.

MAYFIELD, H. F. 1975. Suggestions for calculating nesting success. Wilson Bull. 78: 456-466.

MEYER DE SCHAUENSEE, R. 1970. A guide to the birds of South America. Wynnewood, Pennsylvania, Livingston Publ. Co.

MIDDLETON, A. L. A. 1977. Effect of cowbird parasitism on American Goldfinch nesting. Auk 94: 304-307.

ORIANS, G. H., & H. S. HORN. 1969. Overlap in foods and foraging of four species of blackbirds in the potholes of central Washington. Ecology 50: 930-938.

PEREYRA, J. A. 1938. Aves de la zona ribereña nordeste de la Provincia de Buenos Aires. Mem. Jardín Zool. La Plata: 1-304.

POST, W., & J. W. WILEY. 1976. The Yellow-shouldered Blackbird—present and future. Amer. Birds 30: 13-20.

———. 1977. Reproductive interactions of the Shiny Cowbird and the Yellow-shouldered Blackbird. Condor 79: 176-184.

ROTHSTEIN, S. I. 1971. Observation and experiment in the analysis of interactions between brood parasites and their hosts. Amer. Natur. 105: 71-74.

———. 1975a. An experimental and teleonomic investigation of avian brood parasitism. Condor 77: 250-271.

———. 1975b. Evolutionary rates and host defenses against avian brood parasitism. Amer. Natur. 109: 161-176.

———. 1976. Experiments on defenses Cedar Waxwings use against cowbird parasitism. Auk 93: 675-691.

———. 1982. Successes and failures in avian and nestling recognition with comments on the utility of optimality reasoning. Amer. Zool. 21: 547-560.

SALVADOR, S. A. 1983. Parasitismo de cría del renegrido (*Molothrus bonariensis*) en Villa María, Córdoba, Argentina (Aves: Icteridae). Hist. Nat. 3: 149-158.

SEEL, D. C. 1969. Food, feeding rates and body temperature in the nestling House Sparrow *Passer domesticus* at Oxford. Ibis 111: 36-47.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. New York, McGraw-Hill.

SKUTCH, A. F. 1976. Parent birds and their young. Austin, Texas, Univ. Texas Press.

BROOD PARASITISM IN A HOST GENERALIST, THE SHINY COWBIRD: II. HOST SELECTION

PAUL MASON[1]
Department of Zoology, University of Texas, Austin, Texas 78712 USA

ABSTRACT.—Host selection by brood parasitic Shiny Cowbirds (*Molothrus bonariensis*) was studied at two sites in Buenos Aires Province, Argentina. The eggs of the parasite are either spotted or immaculate, so host selection was studied with respect to egg type as well as to site. Immaculate eggs were rare at both sites. Cowbirds in this region prefer to parasitize nests of birds larger than themselves. This preference contrasts with that of almost all other brood parasites, and even that of Shiny Cowbirds in other parts of the species' range. One large species, the Chalk-browed Mockingbird (*Mimus saturninus*) was used frequently and consistently at both sites. At least two other large species (thrushes) were used at Site I, but neither was present at Site II. Cowbirds were more specialized on large hosts at Site I: only 9% of the spotted eggs were laid in nests of small birds at Site I, whereas 35% were laid in such nests at Site II. Small species, such as the Rufous-collared Sparrow (*Zonotrichia capensis*), were used to a greater extent at Site II than Site I (where some of the same species were not used at all). The shift to smaller hosts is probably a response to a change in the structure of the community; large host species are relatively less abundant at Site II.

Rejecter species are large, and all were parasitized while many smaller accepter species were unmolested. Surprisingly, more immaculate eggs were laid in nests where they had little chance of successful incubation, rather than in nests of accepters. No evidence suggests that host races ("gentes") are formed. To the contrary, female cowbirds laying different egg types apparently select hosts in the same manner. *Received 8 August 1984, accepted 25 July 1985.*

SPECIES that use a wide variety of resources are known as generalists. The brood parasitic Shiny Cowbird (*Molothrus bonariensis*) is an extreme generalist with respect to the "host niche": its eggs have been found in nests of 201 species (Friedmann and Kiff 1985).

Our knowledge of how female cowbirds select hosts is incomplete and biased. First, data on parasitism are often gathered indirectly by studying a particular host species. Information about the composition of the host community and the rates of parasitism of other species is frequently unavailable. A second source of bias concerns the breeding seasons of host and parasite. In Tucumán Province, Argentina, only early nests of the Rufous-collared Sparrow (*Zonotrichia capensis*) escaped parasitism: all late nests were parasitized (King 1973). Third, several Shiny Cowbirds often parasitize a single nest (Friedmann 1929, 1963; Friedmann et al. 1977). The proportion of nests parasitized, the most frequently reported statistic, is an incomplete descriptor of parasitism in this case. A fourth bias concerns parasitism of species that reject cowbird eggs. Because rejecter species generally remove cowbird eggs in a very short time, parasitism of rejecters is unlikely to be observed (Rothstein 1971, 1975, 1977). Experiments simulating parasitism must have been performed previously to identify rejecters.

This study describes and interprets the contrasting patterns of host selection by Shiny Cowbird females at two sites in Buenos Aires Province, Argentina. Geographic variation in host selection remains unexplained. For example, parasitism of the Rufous-collared Sparrow (by the nominate subspecies of the cowbird) varies from 15 to 77% according to site (Sick 1958; King 1973; Fraga 1978, 1983; Gochfeld 1979; Salvador 1983).

I also present data on host selection with regard to egg color. Almost all eggs can be described as spotted or immaculate in eastern Argentina, Uruguay, and portions of Brazil. Intermediate eggs with a few fine spots are rare (Friedmann 1929; Fraga 1978, 1983, 1985; Gochfeld 1979; Salvador 1983). Some host species, dual accepters, incubate both morphs. Other hosts, dual rejecters, remove all cowbird eggs

---

[1] Present address: Department of Biological Sciences, University of California, Santa Barbara, California 93106 USA.

The Auk 103: 61-69. January 1986

from the nest. One major host (Chalk-browed Mockingbird, *Mimus saturninus*) is a differential accepter that ejects immaculate eggs but accepts spotted ones (Fraga 1980, 1985; Mason 1986). Several other important host species probably are differential accepters of cowbird eggs (Friedmann et al. 1977, Fraga 1985). These species are particularly important because they represent strong sources of natural selection on egg morphology and host selection. The ecological situation could potentially result in the evolution of host races or "gentes" (Payne 1977).

METHODS

One season was spent at each of two sites located 17.6 km apart near Magdalena, Buenos Aires Province, Argentina: Site I was Estancia San Isidro and Site II was Estancia El Talar. Further details, including the relative abundance of passerine species, are presented elsewhere (Mason 1985). The first season lasted from 20 October 1977 to 24 February 1978, and the second from 21 September 1978 to 10 February 1979. Very little laying by any passerine species occurs outside this interval (see below and Mason 1985). Nests were observed repeatedly until young fledged or activity at the nest ceased. Observations were carried out daily, although most nests were not observed with such frequency. Shiny Cowbird eggs were scored for color (spotted, immaculate, or intermediate), date, and host. A cohort of nests of the same species at each site was then characterized by a distribution describing the frequency of nests with a certain number of cowbird eggs of a specific type. Distributions obtained in this manner were compared using the heterogeneity *G*-test (Sokal and Rohlf 1981). Other statistical tests vary according to the particular comparison (see below). The diversity of host use at each site was described by calculating the Shannon-Weaver index (Peet 1974, Whittaker 1975).

Scientific names of species are given in the Appendix.

RESULTS

The data base consists of 360 nests (7 nest boxes) of 28 passerine species. I found 233 Shiny Cowbird eggs in nests of 13 species. The distribution of 212 spotted Shiny Cowbird eggs in 333 nests discovered in the egg phase is given in the Appendix. Species are listed by decreasing winglength of adult females (Mason 1980) because more accurate data for body size (i.e. weight) are lacking. Both intensity (mean number of cowbird eggs per parasitized nest) and frequency of parasitism (percentage of nests parasitized) are reported because many nests were multiply parasitized. Eggs laid in peculiar circumstances (such that they could not be scored for acceptance or rejection), and eggs found in nests but later rejected are included.

Only 15 immaculate and 6 intermediate eggs with a few fine spots were seen. Intermediate eggs appear immaculate from a distance of about 1 m or more. The Chalk-browed Mockingbird, the only species known to respond differentially to different egg morphs (Fraga 1985, Mason 1986), apparently perceives intermediate eggs as immaculate (see below).

Comparisons between sites.—Immaculate and intermediate eggs were rare at both sites. At Site I, I found 4 immaculate eggs, 0 intermediate eggs, and 8 spotted eggs in nests of dual accepters. At Site II, I found 0 immaculate eggs, 1 intermediate egg, and 53 spotted eggs in such nests.

At both sites, species larger than the cowbird were preferred as hosts (Site I: $G = 57.6$, 7 df, $P < 0.001$; Site II: $G = 34.0$, 7 df, $P < 0.001$). The mockingbird was the only large species present at both sites and represented by samples sufficient for statistical comparison; it was parasitized equally at each site ($G = 13.3$, 9 df, $P > 0.1$). All thrush nests were parasitized. In addition to the 5 nests found in the egg stage (see Appendix), an additional nest of each species each contained 2 cowbird young.

At Site I, large, abundant passerines (excluding the mockingbird) were: Rufous Hornero (a dual rejecter), Great Kiskadee (response to spotted cowbird eggs uncertain; Mason 1986), Rufous-bellied Thrush, White-rumped Swallow (body size considerably smaller than that of the cowbird, but included because of its winglength), and the Brown-and-yellow Marshbird [*Pseudoleistes virescens*; no nests found, but a frequent host choice in Buenos Aires (Gibson 1918; Hudson 1920; Friedmann 1929, 1963; Friedmann et al. 1977)]. At Site II, the thrush was absent and the Brown-and-yellow Marshbird rare (Mason 1985). Excluding the small-bodied swallow, only 1 large accepter of spotted eggs (the mockingbird) was abundant at Site II, as opposed to at least 2 (mockingbird, thrush) but probably 3 (including the marshbird) such species at Site I.

The sites differed markedly in that species smaller than the cowbird were used to a much greater extent at Site II. The Rufous-collared Sparrow was used significantly more at Site II than at Site I ($G = 9.7$, 3 df, $P < 0.01$). Two other species (Yellow-browed Tyrant, House Wren) were ignored by cowbirds at Site I, but both were parasitized at Site II, although sample sizes are small. The tyrant, wren (natural nest sites), and sparrow were used equally at Site II ($G = 4.4$, 6 df, $P > 0.50$). In addition, the Bay-winged Cowbird was used more at Site II than at Site I, and a single spotted cowbird egg was laid in a nest of the Freckle-breasted Thornbird at Site II the day following loss of that nest. Only 1 small species (Saffron Finch) was parasitized at Site I but not Site II. When frequencies for all small species with data from both sites were pooled, smaller species were parasitized significantly more often ($G = 16.9$, 5 df, $P < 0.005$).

House Wrens at Site II nesting in boxes were more heavily parasitized than those nesting in natural sites ($G = 17.30$, 5 df, $P < 0.05$). A pair of wrens used a nest box at Site I, but this nest was not parasitized. The only other use of a nest box was by a pair of Saffron Finches (Site II).

Cowbirds selected a more diverse array of hosts at Site II than at Site I (measured by the Shannon-Weaver index; Peet 1974, Whittaker 1975), regardless of whether hosts were characterized by species or by size (Table 1). The latter analysis was done because a cowbird's decision to parasitize a nest may be based on some general aspect, such as size, rather than on species identity (Rothstein 1976).

Parasitism of rejecters.—Although I could not estimate the true frequency of parasitism of rejecters, I observed some cowbird eggs in nests of the Rufous Hornero and the Fork-tailed Flycatcher (both dual rejecters; Fraga 1980, Mason 1986). Responses could not be scored in 3 cases of parasitism of the hornero because I accidentally destroyed one nest, or the cowbird egg was laid extremely late in the incubation or nestling period. Two spotted eggs were rejected and later found, one in the entrance of a nest and the other directly below a nest. A broken eggshell was found below another nest, probably from an egg laid and rejected between observations. Four nests of the Fork-tailed Flycatcher contained cowbird eggs. Two nests had 3 cowbird eggs each (1 of which was intermediate), and all eggs were ejected. Neither nest was ever known to contain host eggs. Two other nests each received 1 spotted egg, which was ejected in both cases.

The Chalk-browed Mockingbird, unlike the hornero and the flycatcher, generally rejects immaculate eggs. Thirteen immaculate and intermediate eggs were observed in 10 mockingbird nests. Three were accepted, 7 ejected, and the remainder could not be scored (predation or collection). At one nest where acceptance was observed, an immaculate egg was rejected the previous day.

TABLE 1. Diversity in host selection by site.[a]

	p_i	$-p_i\log p_i$
Host diversity measured by species		
Site I		
Rufous Hornero	0.013	0.024
Cattle Tyrant	0.013	0.024
Chalk-browed Mockingbird	0.759	0.091
Rufous-bellied Thrush	0.127	0.114
Creamy-bellied Thrush	0.013	0.024
Bay-winged Cowbird	0.025	0.040
Saffron Finch	0.013	0.024
Rufous-collared Sparrow	0.038	0.054
		$H' = 0.395$[b]
Site II		
Rufous Hornero	0.022	0.037
Freckle-breasted Thornbird	0.007	0.016
Yellow-browed Tyrant	0.030	0.045
Cattle Tyrant	0.007	0.016
Fork-tailed Flycatcher	0.052	0.067
White-rumped Swallow	0.037	0.053
House Wren	0.059	0.073
House Wren (nest boxes)	0.141	0.120
Chalk-browed Mockingbird	0.533	0.146
Bay-winged Cowbird	0.015	0.027
Rufous-collared Sparrow	0.096	0.098
		$H' = 0.698$
Host diversity measured by size[c]		
Site I		
Large	0.911	0.037
Small	0.089	0.093
		$H' = 0.130$
Site II		
Large	0.644	0.123
Small	0.356	0.160
		$H' = 0.283$

[a] p's represent the proportion of spotted eggs found in nests of different species.

[b] Host diversity measured using the Shannon-Weaver index (Whittaker 1975): $H' = -\Sigma p_i \log p_i$

[c] Large and small reckoned using winglength relative to the Shiny Cowbird.

Rejecter species of South America resemble North American rejecters in being large. Rejecters (of at least one morph) are, on average, larger than accepter species (Table 2; $P < 0.05$, Mann-Whitney $U = 5$; Siegel 1956). This test,

TABLE 2. Passerine size (estimated by winglength) and response to cowbird eggs.

Wing-length[a]	Species	Response to eggs[b]	
		Spotted	Immaculate
138	Brown-chested Martin	Acc	Acc
129	Great Kiskadee[c]	?	Acc
126	Chalk-browed Mockingbird	Acc	Rej
125	Rufous-bellied Thrush[c]	Acc?	Rej?
123	Creamy-bellied Thrush	Acc	Acc
119	White-rumped Swallow	Acc	Acc
112	Fork-tailed Flycatcher	Rej	Rej
107	Rufous Hornero	Rej	Rej
104	Shiny Cowbird		
99	Cattle Tyrant	Acc	Acc
98	Blue-and-yellow Tanager	Acc	Acc
93	Bay-winged Cowbird	Acc	Acc
90	Yellow-browed Tyrant	Acc	Acc
85	Firewood-gatherer	Acc	Acc
81	Vermillion Flycatcher	Acc	Acc
73	House Sparrow	Acc	Acc
71	Grassland Yellow-Finch	Acc	Acc
70	Freckle-breasted Thornbird	Acc	Acc
67	Rufous-collared Sparrow	Acc	Acc
66	Saffron Finch	Acc	Acc
64	Tufted Tit-Spinetail	Acc	Acc
63	Wren-like Rushbird	Acc	Acc
63	Little Thornbird	Acc	Acc
57	Grassland Sparrow	Acc	Acc
51	House Wren	Acc	Acc
51	Masked Gnatcatcher	Acc	Acc
48	White-crested Tyrannulet	Acc	Acc

[a] Rejecters are significantly larger than accepters (Mann-Whitney U-test, $P < 0.05$, $U = 5$). Large and small reckoned relative to the Shiny Cowbird.

[b] Acc = accepts, Rej = rejects (Mason 1986).

[c] Not included in the analysis because response to cowbird eggs not verified experimentally.

based on winglength, is conservative because it includes as large birds two Hirundinidae (White-rumped Swallow, Brown-chested Martin), birds with extremely long wings relative to body size.

Seasonality.—The first cowbird egg was laid on 7 October and the last on 19 January (Fig. 1). Three species, all furnariids (Rufous Hornero, Firewood-gatherer, Freckle-breasted Thornbird), completed a portion of their breeding before the cowbird (Mason 1985). The last two species accept all cowbird eggs (Mason 1986), but only a single nest of the thornbird was parasitized (see Appendix). Nests of the Rufous Hornero were ranked by date: parasitized nests occurred later in the season (Mann-Whitney $U = 8$, $P < 0.025$; Siegel 1956).

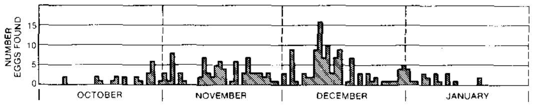

Fig. 1. Dates that cowbird eggs were laid or found.

The breeding seasons of the Chalk-browed Mockingbird and the Rufous-collared Sparrow were completely within the breeding season of the cowbird. I divided the breeding seasons of these two hosts into quarters and tested for heterogeneity among the subsamples. For the mockingbird, I pooled both sites because the distributions were equivalent. For the sparrow, parasitism only from Site II was analyzed. The subsamples provided no evidence of heterogeneity in either species (mockingbird: $G = 27.4$ for 27 df, NS, $0.25 < P < 0.5$; sparrow: $G = 9.2$ for 9 df, NS, $0.25 < P < 0.5$).

DISCUSSION

The extent of generalization by Shiny Cowbirds varied between two sites. Most large species apparently were used consistently, regardless of response to cowbird eggs. Use of smaller species was variable, but more prevalent at Site II. The Chalk-browed Mockingbird was parasitized consistently and heavily at both sites. Other large hosts (thrushes) were parasitized at Site I, but were absent from Site II. The Brown-and-yellow Marshbird, probably a common host in Buenos Aires Province (Hudson 1874, 1920; Sclater and Hudson 1888; Gibson 1918; see reviews by Friedmann 1929, 1963, and Friedmann et al. 1977), was abundant at Site I but rare at Site II.

The Shannon-Weaver indices (Table 1) describe the width of the "host niche" and illustrate differences in site-specific host selection. Although the measurements were determined in part by my ability to find and examine nests, the occasional or rare parasitism of a few species not censused would result in only slight changes. If I missed common, heavily parasitized species, the indices would be substantially altered. The only species likely in this category is the Brown-and-yellow Marshbird at Site I. If this species was heavily parasitized, the index (reckoned by species) would increase at Site I, decreasing the difference between sites. If reckoned by size, however, the index would increase the contrast because the marshbird is a large species (Mason 1980).

Conspicuousness might predispose a nest to parasitism (Brown-headed Cowbird, *Molothrus ater*: Nice 1937, Rothstein 1975; Shiny Cowbird: Friedmann 1929, 1963; Gochfeld 1979), but the contrast between sites in parasitism of the Rufous-collared Sparrow and other small species argues against the importance of conspicuousness. The elaborate nests of furnariids (e.g. the hornero, Firewood-gatherer, and thornbirds) are conspicuous to the human observer, but these are not equally likely to be parasitized. Birds that nest in old hornero nests (Tufted Tit-Spinetail, White-rumped Swallow, Saffron Finch, House Sparrow) were likewise not equally parasitized despite the control for nest site (Appendix; Mason 1985). The strongest support for the conspicuousness argument is the significant difference (at Site II) in parasitism of wrens nesting in boxes as opposed to natural nesting sites.

A more satisfying explanation attributes the local differences to the operation of the same host-selection mechanism in environments offering differing arrays of resources (hosts). Preference measures have different formal descriptions (Ivlev 1961, Murdoch 1969, Rapport and Turner 1970, Chesson 1978, Jaenike 1980), but none can be calculated here because precise numerical densities of host and parasite populations are unavailable. Nonetheless, three distinct lines of evidence provide qualitative support that large hosts are preferred: (1) among accepters, larger hosts were parasitized more frequently and to a greater extent than were smaller hosts; (2) all known rejecter species (which are large) were parasitized while many accepters were left unmolested; and (3) when larger hosts were less abundant or absent, cowbirds used smaller hosts.

Niche expansion and inclusion of species like the sparrow is probably adaptive. Pecking of host eggs by cowbirds is a density-dependent form of mortality that sometimes terminates nesting attempts. Pecking depresses the survivorship of mockingbird nests to a level indistinguishable from that of the Rufous-collared Sparrow (Mason 1986). Presumably, if niche width remained constant in the two environments, nest losses to pecking would further increase at Site II, and cowbirds would experience still lower success.

Other studies share a common feature that supports the claim of a preference for larger hosts: at least one large host is heavily used, while the small Rufous-collared Sparrow is parasitized less. During the last half of a 10-yr study of the sparrow at Lobos, Buenos Aires (Fraga 1978, 1983), parasitism dropped significantly from 72.5 to 43.5%. This coincided with changes in local agriculture that attracted the White-browed Blackbird (*Sturnella superciliaris*), a bird much larger than the sparrow. Two of 6 nests contained cowbird eggs, but the species was seen tending cowbird fledglings (Fraga 1985). Parasitism of the mockingbird remained high (above that of the sparrow; Fraga 1985) and unchanged. In Villa María, Córdoba Province, the mockingbird was used more than any other local host (86.9% of nests parasitized; Salvador 1983). Other large hosts also were used, but only 8 of 22 Rufous-collared Sparrow nests held cowbird eggs. With regard to the parasitism of this host, Salvador wrote: "at this site, it [the sparrow] was not a host of great importance, if we compare it with *Mimus saturninus*" [Salvador 1983: 155 (trans. by PM)].

Gochfeld (1979) found heavy use (23/24 nests) of the Long-tailed Meadowlark (*Sturnella loyca*) but no use (0/11) of the highly similar Lesser Red-breasted Meadowlark (*Sturnella defilippi*) in Bahía Blanca, southern Buenos Aires Province. The low frequency of parasitism of the Rufous-collared Sparrow (2/13 nests) resembles my results at Site I, but 0 of 4 nests of mockingbirds contained cowbird eggs (Gochfeld pers. comm.). Both types of eggs occurred at the site. The absence of parasitic eggs in mockingbird and Lesser Red-breasted Meadowlark nests may possibly reflect rejection behavior of the hosts rather than avoidance by cowbirds.

The preference for large hosts, a trait unusual in any parasitic bird (Payne 1977), may be a phenomenon restricted to the Río de La Plata basin and surrounding area. In the West Indies, there is no clear relationship between host size and preference ranking by Shiny Cowbirds. In Trinidad the diminutive House Wren may be the most highly preferred host (Manolis 1982), while in Puerto Rico both large and small hosts may be heavily used (Pérez Rivera 1983, Wiley 1985).

Host selection by females laying contrasting egg types.—Only 5 immaculate and intermediate eggs were laid in nests of accepters, whereas 16 were laid in nests of species that normally reject these morphs. Females that lay these eggs clearly do not place them preferentially in nests where the eggs will be accepted. No evidence suggests that host selection varies between females.

Fraga (1985) also described immaculate eggs laid in and rejected from mockingbird nests. He estimated that at least one-third of the nests were parasitized with white eggs. Descriptions of immaculate eggs below, but spotted eggs inside, nests of the Brown-and-yellow Marshbird (Hudson 1874, 1920; Sclater and Hudson 1888) suggest that this host is a differential accepter like the mockingbird and that cowbirds behave the same toward the marshbird and the mockingbird. This pattern of host selection is apparently stable because Hudson's observations were conducted more than a century ago.

Parasitism of rejecters.—Parasitism of rejecter species poses a significant and interesting evolutionary problem. Selection penalizes females that lay either egg morph when they lay in nests of dual rejecters. However, oviposition in nests of differential accepters penalizes only certain females. The situation is complex because selection occurs on a phenotype (the morphology of the egg) that is a product of the maternal genotype.

The frequency of oviposition in nests of rejecters suggests that host race formation does not occur in Shiny Cowbirds. Females that lay in nests of rejecters almost certainly did not fledge from nests of those species. Similarly, it seems unlikely that all females laying immaculate eggs in mockingbird nests hatched from spotted eggs laid in mockingbird nests, although this possibility cannot be ruled out. In addition, production of cowbird offspring may be highest for hosts of low-preference ranking. Fraga (1985) presented data that more cowbirds fledged from nests of Rufous-collared Sparrows than of Chalk-browed Mockingbirds, and he argued that most females laying in mockingbird nests probably fledged from nests of other species.

The host selection mechanism is clearly under natural selection, but response to selection requires (among other things) that there exist proximate cues for ultimate success. Apparently, these cues are often lacking, at least in this environment. Some features of Shiny Cowbird parasitism, such as inclusion of the sparrow in the array of host choices, appear to be subtle adaptations (Mason 1986). Other features, such as the parasitism of rejecters, remain perplexing.

ACKNOWLEDGMENTS

M. Christie helped get my research program started. J. M. Gallardo (Director) and J. R. Navas (Jefe, Divisi6n de Ornitología) give me free access to the collections of the Museo Argentino de Ciencias Naturales, Buenos Aires. I am indebted to the estancieros, E. M. and D. Earnshaw (Estancia San Isidro) and A. Landa (Estancia El Talar), for allowing me to work on their land. They and their families showed me the greatest hospitality. R. M. Fraga offered helpful suggestions and encouragement at all stages of the research. M. Gochfeld provided a list of nests he found at Bahía Blanca. Earlier versions of the manuscript were read and criticized by A. M. Dufty, Jr., R. M. Fraga, M. Gochfeld, W. W. Murdoch, S. I. Rothstein, and S. S. Sweet. Their comments have considerably improved the final version. The Frank M. Chapman Fund of the American Museum of Natural History provided partial financial support. I was supported by NSF grant BSR 82-14999 to S. I. Rothstein during the preparation of the manuscript. Finally, I would like to acknowledge H. Friedmann, whose 1929 monograph and subsequent publications served as my initial inspiration to undertake this project.

LITERATURE CITED

CHESSON, J. 1978. Measuring preference in selective predation. Ecology 59: 211-215.

FRAGA, R. M. 1978. The Rufous-collared Sparrow as a host of the Shiny Cowbird. Wilson Bull. 90: 271-284.

———. 1980. The breeding of Rufous Horneros (*Furnarius rufus*). Condor 82: 58-68.

———. 1983. Parasitismo de cría del renegrido (*Molothrus bonariensis*) sobre el chingolo (*Zonotrichia capensis*): nuevas observaciones y conclusiones. Hornero 12, No. Extraord.: 245-255.

———. 1985. Host-parasite interactions between Chalk-browed Mockingbirds and Shiny Cowbirds. Pp. 829-844 *in* Neotropical ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithol. Monogr. No. 36.

FRIEDMANN, H. 1929. The cowbirds: a study in the biology of social parasitism. Baltimore, C. C. Thomas.

———. 1963. Host relations of the parasitic cowbirds. U.S. Natl. Mus. Bull. 233: 1-276.

———, & L. F. KIFF. 1985. The parasitic cowbirds and their hosts. Proc. West. Found. Vert. Zool. 2: 226-302.

———, ———, & S. I. ROTHSTEIN. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contr. Zool. 235: 1-75.

GIBSON, E. 1918. Further ornithological notes from the neighbourhood of Cape San Antonio, Province of Buenos Ayres. Ibis 4, 4th Ser.: 1-38.

GOCHFELD, M. 1979. Brood parasite and host coevolution: interactions between Shiny Cowbirds and two species of meadowlarks. Amer. Natur. 113: 855-870.

HUDSON, W. H. 1874. Notes on the procreant instincts of the three species of *Molothrus* found in Buenos Ayres. Proc. Zool. Soc. London: 153-174.

———. 1920. Birds of La Plata, vol. 1. New York, E. P. Dutton.

IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes (D. Scott, trans.). New Haven, Connecticut, Yale Univ. Press.

JAENIKE, J. 1980. A relativistic measure of variation in preference. Ecology 61: 990-997.

KING, J. R. 1973. Reproductive relationships of the Rufous-collared Sparrow and the Shiny Cowbird. Auk 90: 19-34.

MANOLIS, T. D. 1983. Host relationships and reproductive strategies of the Shiny Cowbird in Trinidad and Tobago. Unpublished Ph.D. dissertation, Boulder, Colorado, Univ. Colorado.

MASON, P. 1980. Ecological and evolutionary aspects of host selection in cowbirds. Unpublished Ph.D. dissertation, Austin, Texas, Univ. Texas.

———. 1985. The nesting biology of some passerines of Buenos Aires, Argentina. Pp. 954-972 *in* Neotropical ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithol. Monogr. No. 36.

———. 1986. Brood parasitism in a host generalist, the Shiny Cowbird: I. The quality of different species as hosts. Auk 103: 52-60.

MURDOCH, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Monogr. 39: 335-354.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow, part I. Trans. Linnaean Soc. New York 4: 1-247.

PAYNE, R. B. 1977. The ecology of brood parasitism in birds. Ann. Rev. Ecol. Syst. 8: 1-28.

PEET, R. K. 1974. The measurement of species diversity. Ann. Rev. Ecol. Syst. 5: 285-307.

PÉREZ RIVERA, R. A. 1983. An account of bird parasitism by the Shiny Cowbird in Puerto Rico. El Cóndor: revista de la Universidad del Turabo 8: 57-71.

RAPPORT, D. J., & J. E. TURNER. 1970. Determination of predator food preferences. J. Theoret. Biol. 26: 365-372.

ROTHSTEIN, S. I. 1971. Observation and experiment in the analysis of interactions between brood parasites and their hosts. Amer. Natur. 105: 71-74.

———. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77: 250-271.

———. 1976. Cowbird parasitism of the Cedar Waxwing and its evolutionary implications. Auk 93: 498-500.

———. 1977. Cowbird parasitism and egg recognition of the Northern Oriole. Wilson Bull. 89: 21-32.

SALVADOR, S. A. 1983. Parasitismo de cría del renegrido (*Molothrus bonariensis*) en Villa María, Córdoba, Argentina (Aves: Icteridae). Hist. Nat. 3: 149-158.

SCLATER, P. L., & W. H. HUDSON. 1888. Argentine ornithology. Vol. 1, Passeres. London, R. H. Porter.

SICK, H. 1958. Notas biológicas sôbre o gaudério, "*Molothrus bonariensis*" (Gmelin) (Icteridae, Aves). Rev. Brasil. Biol. 18: 417-431.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. New York, McGraw-Hill.

SOKAL, R. R., & F. J. ROHLF. 1981. Biometry, 2nd ed. San Francisco, W. H. Freeman.

WHITTAKER, R. H. 1975. Communities and ecosystems, 2nd ed. New York, Macmillan Publ. Co.

WILEY, J. W. 1985. Shiny Cowbird parasitism in two avian communities in Puerto Rico. Condor 87: 165-176.

APPENDIX. Parasitized and unparasitized nests.

Wing-length[a]	Species	No. of cowbird eggs per nest[b]											Freq.[c]	Int.[d]
		0	1	2	3	4	5	6	7	8	9	10		
	A. Distribution, frequency, and intensity of parasitism													
126	Chalk-browed Mockingbird (*Mimus saturninus*)													
	Site I (n = 30)	8	8	6	5	0	0	0	1	1	0	1	0.73	2.73
	Site II (n = 38)	10	9	6	6	3	3	1					0.74	2.57
125	Rufous-bellied Thrush (*Turdus rufiventris*)													
	Site I (n = 4)	0	2	1	0	0	1						1.00	2.25
	Site II	Species absent												
123	Creamy-bellied Thrush (*T. amaurochalinus*)													
	Site I (n = 1)	0	1										1.00	1.00
	Site II	Species absent												
119	White-rumped Swallow (*Tachycineta leucorrhoa*)													
	Site I (n = 1)	1											0.00	—
	Site II (n = 9)	5	3	1									0.44	1.25
112	Fork-tailed Flycatcher (*Tyrannus savana*)[e]													
	Site I	No nests examined												
	Site II (n = 7)	3	2	1	1								0.57	1.75
107	Rufous Hornero (*Furnarius rufus*)[e]													
	Site I (n = 1)	0	1										1.00	1.00
	Site II (n = 16)	13	3										0.19	1.00
104	Shiny Cowbird (*Molothrus bonariensis*)													
99	Cattle Tyrant (*Machetornis rixosus*)													
	Site I (n = 1)	0	1										1.00	1.00
	Site II (n = 2)	1	1										0.50	1.00
93	Bay-winged Cowbird (*Molothrus badius*)													
	Site I (n = 10)	8	2										0.20	1.00
	Site II (n = 5)	3	2										0.40	1.00
90	Yellow-browed Tyrant (*Satrapa icterophrys*)													
	Site I (n = 2)	2											0.00	—
	Site II (n = 8)	4	4										0.50	1.00
70	Freckle-breasted Thornbird (*Phacellodomus striaticollis*)													
	Site I (n = 3)	3											0.00	—
	Site II (n = 4)	3	1										0.25	1.00
67	Rufous-collared Sparrow (*Zonotrichia capensis*)													
	Site I (n = 32)	29	3										0.09	1.00
	Site II (n = 19)	11	5	1	2								0.42	1.63
66	Saffron Finch (*Sicalis flaveola*)													
	Site I (n = 13)	12	1										0.08	1.00
	Site II (n = 22)	22											0.00	—

APPENDIX. Continued.

Wing-length[a]	Species	No. of cowbird eggs per nest[b]												
		0	1	2	3	4	5	6	7	8	9	10	Freq.[c]	Int.[d]
51	House Wren (*Troglodytes aedon*)													
	Natural nest sites													
	Site I (*n* = 3)	3											0.00	—
	Site II (*n* = 8)	3	3	1	1								0.63	1.60
	Nest boxes													
	Site I (*n* = 1)	1											0.00	—
	Site II (*n* = 5)	0	0	2	0	2	0	0	1				1.00	3.80
	B. Species not observed to be parasitized[f]													
138	Brown-chested Martin (*Phaeoprogne tapera*) (0, 1)													
129	Great Kiskadee (*Pitangus sulphuratus*)[e] (0, 7)													
85	Firewood-gatherer (*Anumbius annumbi*) (0, 11)													
81	Vermillion Flycatcher (*Pyrocephalus rubinus*) (0, 22)													
73	House Sparrow (*Passer domesticus*) (0, 3)													
71	Grassland Yellow-Finch (*Sicalis luteola*) (0, 3)													
69	Hooded Siskin (*Carduelis magellanica*) (0, 7)													
64	Tufted Tit-Spinetail (*Leptasthenura platensis*) (1, 3)													
63	Wren-like Rushbird (*Phleocryptes melanops*) (0, 22)													
63	Little Thornbird (*Phacellodomus sibilatrix*) (1, 0)													
57	Grassland Sparrow (*Ammodramus humeralis*) (0, 1)													
51	Masked Gnatcatcher (*Polioptila dumicola*) (0, 1)													
48	White-crested Tyrannulet (*Serpophaga subcristata*) (1, 3)													
?	Tropical Kingbird (*Tyrannus melancholicus*) (1, 0)													
?	Pipit (*Anthus* sp.) (0, 1)													

[a] Species listed by decreasing winglength (measured from skins of adult females collected in Buenos Aires Province; Mason 1980).

[b] Spotted eggs only.

[c] Freq. = frequency (proportion of nests parasitized).

[d] Int. = intensity (mean number of eggs per parasitized nest).

[e] *Tyrannus savana* and *Furnarius rufus* rejected cowbird eggs. *Pitangus sulphuratus* may show intermediate levels of rejection. Some birds were not tested for response to cowbird eggs (Mason 1986).

[f] Sample sizes for sites I and II in parentheses.

REVERSED SEXUAL SIZE DIMORPHISM: EFFECT ON RESOURCE DEFENSE AND FORAGING BEHAVIORS OF NONBREEDING NORTHERN HARRIERS

ETHAN J. TEMELES

Department of Zoology, University of California, Davis, California 95616 USA

ABSTRACT.—Sexual differences in resource defense and foraging behaviors during the nonbreeding season are detailed for Northern Harriers (*Circus cyaneus*) in California. Female harriers hunted more frequently in high (>0.5 m) vegetation than males. In addition, females hunted at slower speeds and used different hunting behaviors than males. Females in high vegetation showed a significantly greater response (i.e. attack) rate to approaching harriers than males, and females won nearly all (28/29) aggressive interactions with males. These results suggest that sexual differences in harrier foraging behavior during the nonbreeding season result from females excluding males from preferred foraging areas and males adopting alternative foraging strategies. Foraging strategies of harrier sexes are compared with foraging strategies of sexes of birds in which males are larger than females to examine the role of body size in determining sexual foraging strategies. *Received 7 March 1985, accepted 2 July 1985.*

IN many bird species (e.g. ducks, hummingbirds, woodpeckers), sexes differ in geographic distribution, habitat use, or foraging behavior during the nonbreeding season (Ligon 1968, Feinsinger and Colwell 1978, Hogstad 1978, Stiles and Wolf 1979, Kilham 1983, Hepp and Hair 1984). Social dominance is one mechanism that may influence nonbreeding sexual foraging differences (Gauthreaux 1978). Usually, social dominance confers priority of access to resources (e.g. food) and is attained by those individuals that are most successful in aggressive interactions (e.g. fights, chases) with others (Morse 1980).

Social dominance during the nonbreeding period affects access to preferred resources and leads to sexual foraging differences in many avian species (see above references). In general, larger males supplant smaller females and forage in areas of highest resource density; these sexual differences in foraging area often are accompanied by sexual differences in foraging behavior when foraging behaviors vary with habitat type. Alternatively, smaller females may adopt different foraging behaviors to exploit the same resources as dominant males. Both patterns of sex-specific foraging during the nonbreeding season are well illustrated in many hummingbird species: larger (heavier), socially dominant males defend high-quality food territories, whereas smaller (lighter), socially subordinate females trapline-forage among dispersed resources, defend poorer-quality territories, or "rob" male territories (Stiles 1973, Wolf et al. 1976, Feinsinger and Colwell 1978, Kodric-Brown and Brown 1978, Stiles and Wolf 1979, Kuban and Neill 1980, Kuban et al. 1983).

I examined the consequences of sexual size reversal on social dominance and sex-specific foraging behavior in the Northern Harrier (*Circus cyaneus*). Females are considerably larger than males in this species, as in virtually all species of predatory birds (Falconiformes, Strigiformes, Stercorariidae). Sexual differences in distribution, habitat use, or foraging behavior during the nonbreeding season have been recorded for harriers (Schipper et al. 1975, Bildstein 1978, Bildstein et al. 1984) as well as for other raptors (Mills 1976, Stinson et al. 1981, Marquiss and Newton 1982) and for nonraptorial species in which females are larger than males (e.g. Puttick 1981). However, female social dominance as the mechanism responsible for these differences has only been hypothesized or inferred (Mills 1976, Mueller et al. 1977, Evans 1980, Boxall and Lein 1982) or deduced from experimental introduction of a captive bird into the territory of a resident bird (e.g. Cade 1955).

I present data on harriers that show that sexual differences in foraging area and behavior during the nonbreeding season are due to females aggressively excluding males from preferred foraging areas. I then examine the influence of body size on sex-specific foraging strategies by comparing the foraging behaviors of harrier sexes to foraging behaviors of sexes of birds in which males are larger than females.

STUDY AREA AND METHODS

The 25-km^2 study area was located 3 km northeast of Davis, Yolo Co., California. This area is primarily agricultural cropland composed of the following vegetation types: corn stubble, rice stubble, winter wheat, winter-wheat stubble, plowed field, and fallow field. The observations reported here were part of a long-term study of harrier foraging behavior and cover the period 29 November 1983 to 31 January 1984. These dates were not arbitrarily chosen: harriers began to defend areas in late November and ceased to defend areas in early February (observations in the winter of 1984-1985 corroborate this). I made 20 days of observations involving 8 h of field time per day.

When a foraging harrier was sighted, I recorded the date and time of each observation, the sex and age of the bird, the vegetation type and height, hunting speed (where possible), and hunting behavior (where possible). Adult harriers were easily and unambiguously sexed: adult males are gray dorsally and adult females are brown. Juvenile *C. c. hudsonius* could be distinguished from adult females by their rufous, unstreaked underbelly (Cramp and Simmons 1980). Extreme sexual size dimorphism also facilitated sexing harriers of all ages, especially on occasions when a bird was seen flying with a member of the opposite sex. Because the number of juveniles (= rufous-breasted birds) seen on the study area was extremely low (9 juveniles compared with 153 adults, or 6%), and because studies indicate that foraging of juvenile birds differs from adults (e.g. Marr and McWhirter 1982), I excluded juveniles from the data analyses.

Vegetation types were classified into two categories on the basis of height. Vegetation was described as "high" in fallow fields where all vegetation was >0.5 m high and as "low" in corn, rice, and winter-wheat stubble, winter-wheat fields, and plowed fields where all vegetation was <0.5 m high ($n = 500$ measurements of vegetation height, measured from ground surface to top of plant). Although vegetation type and height were the variables of primary interest for statistical analyses, differences in vegetation type and height also were associated with differences in vegetation density: vegetation in high, fallow fields was much denser than vegetation in low, stubble fields, where rows were separated by 7-10 cm of open space ($n = 500$ measurements of vegetation density, i.e. distances between adjacent plants).

Hunting speeds of harriers were recorded on an automobile speedometer. To insure reliability and consistency of measurement with this technique, I recorded hunting speeds of harriers only when driving parallel to them for a period of >30 s. These measurements were possible owing to the number of roads crossing the study area and the harriers' acceptance of moving automobiles. Because I found that harriers altered their hunting behavior during periods of high winds, I excluded from my analyses those observations of harriers made when wind speeds exceeded 16 km/h. I recognized three categories of hunting speeds: (1) ≤ 8 km/h, (2) 16-24 km/h, and (3) ≥ 32 km/h. Following Schipper et al. (1975) and Bildstein (1978), I classified a harrier's hunting behavior in one of three categories: (1) straight flight [less than 5 sharp ($>30°$) turns/min] through a field, (2) quartering (more than 5 sharp turns/min) back and forth over a field, and (3) border (edge) following (e.g. hunting along ditches, fence rows, road shoulders). I did not record subsequent observations of a particular sex at a site on the same day unless two or more birds of the same sex were observed simultaneously.

In addition to the general observations described above, I made detailed observations of a smaller number of harriers to obtain a better understanding of their foraging behaviors. In this set of observations, each individual harrier was watched for a 30-min focal period (Altmann 1974). During each 30-min period, I recorded the number of prey capture attempts, the number of successful captures, the type of prey, the time spent in foraging, perching, eating, or in aggressive interactions, the total area foraged in, the number of approaches by male/female conspecifics, and the number of interactions with male/female conspecifics and outcome.

I defined a capture attempt as an effort by a harrier to catch a specific prey item; repeated strikes during the pursuit of a single prey item were considered to represent a single capture attempt. Capture success was defined as the percentage of all capture attempts that ended in prey capture (see Temeles 1985). Several features of my study area and the behaviors of harriers allowed me to accurately identify the types of prey (birds, rodents) attacked. First, birds "flush" out of vegetation when attacked by harriers, whereas rodents do not, and because the vegetation on my study site (even in the high areas) never exceeded 1.2 m and most observations were made at distances of less than 100 m, it was possible to see avian prey as they escaped harriers' attacks. Second, on many occasions harriers picked up vole "nests" while executing unsuccessful capture attempts. Third, harriers often utilize different attack strategies for birds and rodents [e.g. they "pounce" at birds in more rapid motions; Schipper et al. (1975), Bildstein (1978); pers. obs.].

All time observations were recorded on a stopwatch or measured from tape-recorder playbacks. By

TABLE 1. Morphology of 10 male and 10 female adult Northern Harriers in the Louisiana State University Museum of Zoology collection. Data are means ± SD.

Measurement	Male	Female	P
Wing chord (mm)	346.4 ± 9.02	383.9 ± 7.68	<0.001
Bill chord (mm)	16.4 ± 0.70	19.3 ± 0.42	<0.001
Middle toe length (mm)	34.9 ± 1.45	41.2 ± 1.03	<0.001
Hallux claw arc (mm)	22.5 ± 0.67	27.6 ± 1.37	<0.001

using different number combinations and colors of surveyor's tape tied on many markers (e.g. fence wires) at regular intervals on flat land, I estimated foraging areas hunted in by harriers. Distances between markers were measured using a 100-m field tape measure or, in cases where the layout of roads permitted, an automobile odometer. Odometer measurements were checked for accuracy against tape measurements and revealed no differences. Foraging areas were measured after each focal period.

I defined an approach as any harrier (male or female) coming within 100 m of the focal bird. I recognized four different harrier aggressive behaviors, which I placed into two categories on the basis of presence or absence of physical contact. Noncontact behaviors were (1) *Chase*, in which the focal bird flew at the approaching bird and then flew after the approaching bird as it fled, from behind and *on level* with it; and (2) *Escort*, in which the focal bird flew at the approaching bird and then flew after the approaching bird as it fled, from behind and *below* it, both birds flying far out of the focal bird's foraging area (see Bildstein and Collopy 1985). Chase and escort behaviors differed at a quantitative as well as a qualitative level; escorts were considerably longer than chases ($P < 0.001$, t-test; mean ± SD escort = 35.3 ± 14.2 s, $n = 30$; mean ± SD chase = 18.3 ± 8.9 s, $n = 21$; no sex differences). Contact behaviors were (1) *Short contact*, in which the focal bird flew at and then hit or talon-grappled with the approaching bird; and (2) *Long contact*, in which the focal bird flew at and then repeatedly hit and grappled with the approaching bird, both birds falling to the ground several times. Long and short contact behaviors also differed considerably in length ($P < 0.001$, t-test; mean ± SD long = 65.0 ± 17.5 s, $n = 8$; mean ± SD short = 19.2 ± 9.2 s, $n = 6$; females only). I defined a winner of an aggressive encounter as a bird that succeeded in driving the other bird (= loser) out of the foraging area within 2 min after initiation of the encounter. In addition, I recorded other aggressive interactions observed (outside of focal samples).

For purposes of statistical independence of data, I attempted to minimize repeat observations of the same individual in two ways. First, I tried to identify as many individuals as possible by noting plumage characteristics (e.g. missing or damaged feathers) and favorite perch sites. Second, my observations of harriers that could be positively identified indicated that they generally did not utilize the same area for more than 14 days. Consequently, I never made a focal observation of a harrier if a previous focal observation had been made of a harrier of the same sex in the same area within 14 days, unless the new individual differed noticeably in plumage from the old individual. Nonparametric statistical procedures follow Daniel (1978) and Siegel (1956); parametric statistical procedures follow Snedecor and Cochran (1967). Significance levels were determined from tables in Hald (1952).

RESULTS

Morphology.—Size differences between sexes of the North American race *C. c. hudsonius* are highly significant (Table 1; $P < 0.001$). Cramp and Simmons (1980) presented morphological measurements for the European subspecies *C. c. cyaneus* and verified that all sexual size differences are significant. Smaller body weights and winglengths of males corresponded to smaller wing loading and a large difference in the estimated metabolic cost of flight (Table 2).

Habitat use and hunting speeds.—Sexes differed with respect to vegetation height, where the distributions were 83 females and 21 males in high (>0.5 m) vegetation, and 25 females and 24 males in low (<0.5 m) vegetation ($\chi^2 = 13.3$, df = 1, $P < 0.0005$). Females were observed to hunt more often at slow (≤8 km/h) speeds, whereas males were observed to hunt more often at higher (≥16 km/h) speeds ($\chi^2 = 42.2$, df = 2, $P < 0.0005$; number of observations of each sex at given speeds, ≤8 km/h: 34 females, 1 male; 16–24 km/h: 6 females, 15 males; ≥32 km/h: 1 female, 11 males). The sexual differences in hunting speeds were associated with vegetation heights. In high vegetation, 31/32 females observed were hunting at speeds ≤8 km/h, whereas 16/16 males observed were hunting at speeds ≥16 km/h ($\chi^2 = 43.8$, df = 1, $P < 0.0005$). In contrast, there were no significant differences between the sexes for hunting speeds in low vegetation. Moreover, sexes of

TABLE 2. Measurements of winglength, body weight, and wing loading and calculated minimum power required to fly, P_{min} (W, 1 W = 1 J/s) for sexes of Northern Harriers.

Sex	Winglength[a] (m)	Body wt[a] (kg)	Wing loading[b] (g/cm²)	P_{min}[c]
Male	0.344 (20)[d]	0.350 (90)	0.270 (2)	3.02
Female	0.385 (20)	0.531 (97)	0.315 (2)	5.12

[a] Data from Snyder and Wiley (1976).

[b] Average wing loading from data in Poole (1938) and Brown and Amadon (1968).

[c] P_{min} calculated from Pennycuick's (1972) equations. Wing span, b, was estimated from Greenewalt (1962), where $b = 2(\text{winglength})/0.62$. Air density at sea level was used (1.22 kg/m³).

[d] Sample sizes are given in parentheses.

TABLE 3. Hunting areas (km²) determined during 30-min focal observations of Northern Harriers by sex and vegetation height class. n = sample size.

Sex	Vegetation height class	Hunting area		n
		Median	Mean ± SD	
Female	High	0.149	0.185 ± 0.147	16
	Low	0.932	1.018 ± 0.245	3
Male	High	1.126	0.977 ± 0.340	4
	Low	1.087	0.964 ± 0.405	4

harriers showed opposite results in the relation of hunting speed to vegetation height. Hunting speeds of female harriers were negatively associated with vegetation height: 31/34 observations of females hunting at speeds ≤8 km/h were in high vegetation, whereas 6/7 observations of females hunting at speeds ≥16 km/h were in low vegetation ($\chi^2 = 15.8$, df = 1, $P < 0.0005$). Hunting speeds of male harriers were positively associated with vegetation height: 10/16 observations of males hunting at speeds ≤24 km/h were in low vegetation, whereas 10/11 observations of males hunting at speeds ≥32 km/h were in high vegetation (Fisher exact test, two-tailed, $0.01 < P < 0.02$).

Hunting behavior and habitat.—Females were observed to hunt most often by quartering. Males hunted by straight-flying or border-following ($\chi^2 = 42.7$, df = 2, $P < 0.0005$; number of observations of each sex using given behaviors, quarter: 40 females, 2 males; straight flight: 5 females, 26 males; border-following: 16 females, 10 males). The relation among sex, hunting behavior, and vegetation height paralleled the relation among sex, hunting speed, and vegetation height. Sexual differences in hunting behaviors also were associated with high vegetation. In high vegetation, 40/44 females were observed to hunt by quartering, whereas 20/22 males were observed to hunt by straight-flying and border-following ($\chi^2 = 42.4$, df = 1, $P < 0.0005$). No significant differences between the sexes were observed for distributions of hunting behaviors in low vegetation. Quartering by female harriers was associated with vegetation height: 40/44 females observed in high vegetation hunted by quartering, whereas 17/17 females observed in low vegetation hunted by straight-flying and border-following ($\chi^2 = 44.9$, df = 1, $P < 0.0005$).

Hunting areas.—Hunting areas (as determined during each 30-min focal observation) are presented for harrier sexes with respect to vegetation height in Table 3. A Kruskal-Wallis ANOVA of the medians of these hunting areas, with sex and vegetation height classes (e.g. females observed in high vegetation) as factor levels, was highly significant ($H = 18.0$, $P < 0.005$; $n = 27$ different individuals). Two-tailed nonparametric multiple comparisons indicated that the median of the hunting areas of female harriers in high vegetation was significantly smaller than the median of the hunting areas of male harriers in high or low vegetation, or female harriers in low vegetation ($P < 0.05$ overall).

Capture attempts.—Capture rates varied between harrier sexes with respect to vegetation height (Table 4). A Kruskal-Wallis ANOVA of median capture rates, with sex and vegetation height classes as factor levels, was highly significant ($H = 12.6$, $0.005 < P < 0.01$; $n = 32$ different individuals). Female harriers that hunted in high vegetation had significantly more capture attempts per minute than female harriers hunting in low vegetation ($0.01 < P < 0.05$ overall; two-tailed nonparametric multiple comparisons) and tended to have more capture attempts per minute than male harriers hunting in high or low vegetation (Table 4).

Capture success.—Capture successes for different prey types are presented for harrier sexes with respect to vegetation height in Table 5. No significant differences in harriers' capture successes were observed between sexes within vegetation height classes, between sexes, between vegetation height classes, or between prey types (i.e. birds, rodents), but capture suc-

TABLE 4. Number of prey capture attempts per minute of hunting by Northern Harriers with respect to sex and vegetation height class. n = sample size.

Sex	Vegetation height class	No. of attempts per min hunt: Median	No. of attempts per min hunt: Mean ± SD	n
Female	High	0.50	0.53 ± 0.34	16
	Low	0.00	0.15 ± 0.37	7
Male	High	0.04	0.05 ± 0.05	4
	Low	0.00	0.05 ± 0.06	5

TABLE 5. Capture successes of Northern Harriers with respect to sex and vegetation height class for different prey types. Numerators are number of successful attempts, denominators are total number of attempts.

Sex	Vegetation height class	Prey type: Rodents	Prey type: Pheasants	Prey type: Small birds
Female	High	7/111	0/11	0/2
	Low	0/3	—	0/2
Male	High	1/14	—	0/1
	Low	—	—	0/4

cesses were extremely low [overall capture success, rodents: 8/128 (6.25%), birds: 0/20 (0%)]. When hunting attempts by harrier sexes within each vegetation height class were combined, a significant difference in the distribution of attempts at prey types was observed between vegetation height classes. The distributions were 125 and 3 attacks at rodents in high and low vegetation, respectively, and 14 and 6 attacks at birds in high and low vegetation, respectively ($\chi^2 = 18.6$, df = 1, $P < 0.0005$).

Aggressive interactions.—Physical contact occurred more frequently in female-female aggressive interactions than in female-male aggressive interactions; 14/40 female-female interactions involved contact, whereas only 2/29 female-male interactions involved contact (Table 6; $\chi^2 = 7.5$, df = 1, $P < 0.01$). The difference between harrier sexes was also significant in the outcomes of aggressive interactions: in female-female interactions, a female that drove her opponent out of the foraging area within 2 min from the start of the interaction was identified in 19/40 interactions, whereas in female-male interactions, females won 28/29 interactions ($\chi^2 = 18.6$, df = 1, P < 0.0005). Too few male-male interactions ($n = 3$) were observed for statistical analyses (see Table 6).

From the above data (especially the paucity of male-male interactions), I tentatively concluded that typically only females defended foraging areas. However, the low frequency of male interactions could have been the result of differences between the sexes in approach frequencies. To clarify this issue, I examined approach and attack frequencies for focal birds with respect to sex and vegetation height (i.e. foraging area). No significant differences were found in approach frequencies (number of approaches/30 min) with respect to sex and vegetation height (Table 7; Kruskal-Wallis ANOVA corrected for ties, $H_c = 1.8$, $P > 0.1$; $n = 36$ different individuals). Responses *to* approaching harriers did differ significantly among sex-vegetation height factor levels (Table 8; Kruskal-Wallis ANOVA, $H = 13.8$, $0.001 < P < 0.005$; $n = 27$ different individuals). The median response rate (number of attacks/30 min) of females in high vegetation (median = 2) was significantly higher ($P < 0.05$ overall; two-tailed nonparametric multiple comparisons) than median response rates of males in high (median = 0) or in low vegetation (median = 0). To summarize, females won virtually all aggressive interactions with males, and although both sexes were approached by conspecifics at the same rate, only females usually responded to approaches by conspecifics.

DISCUSSION

Frequency of aggression in wintering raptors.—Harrier sexes differ in degree of resource defense, with females typically defending, and males typically not defending, foraging areas. The aggressive interactions I observed may be attributed to high harrier densities and high, concentrated prey densities. Harriers were extremely abundant in the study area. Densities of 8 harriers/km^2 and 15 raptors/km^2 were common, especially in high-vegetation areas. These high raptor densities may have resulted in more frequent aggressive interactions. A similar situation was reported for Snowy Owls (*Nyctea scandiaca*; Evans 1980). Probably, these high raptor densities occurred in response to either high or nonuniform (or both) prey densities within the study area (Snyder and Snyder 1970, Newton 1979). However, under most circumstances prey densities may not be high

TABLE 6. Number of observations of inter- and intrasexual aggressive interactions of nonbreeding Northern Harriers. Male-male interactions (2 escorts, 1 chase) are not included. Also not included are 2 avoidance movements by males at the approach of females.

Sexes	Chase	Escort	Short contact	Long contact
Female-female	13	13	6	8
Female-male	8	17	1	1

TABLE 7. Number of approaches by conspecifics to individual Northern Harriers per 30-min focal observation by sex and vegetation height class. n = sample size.

Sex	Vegetation height class	No. of approaches		n
		Median	Mean ± SD	
Female	High	1.50	1.72 ± 1.32	18
	Low	1.00	1.22 ± 1.09	9
Male	High	1.00	1.00 ± 1.00	5
	Low	1.50	1.25 ± 0.50	4

enough for raptors to be concentrated in one area, and hence aggressive interactions between individuals may occur so infrequently as to be rarely or never recorded. In addition, degree of aggression has been shown to vary with resource quantity or quality (Ewald and Carpenter 1978, Frost and Frost 1980). Consequently, interactions between raptors may be much less overt than in this study and may take the form of avoidance (rather than aggressive) behaviors, which are more difficult to discern. These are important points to consider in understanding sexual differences in wintering distributions of birds, because failure to observe overt, aggressive interactions may not necessarily indicate an absence of social dominance.

Sexual differences in foraging areas.—These results support the view that niche differences between nonbreeding harrier sexes arise from female dominance. I suggest that female dominance conferred priority of access to preferred resources (i.e. the high-vegetation areas) and that as a result of female attacks, male harriers and subordinate females shifted from preferred to less-preferred foraging areas in low vegetation. Some evidence supports the conclusions that the high-vegetation areas defended by females were preferred and that subordinates were forced to forage elsewhere. For example, females in high vegetation hunted over much smaller foraging areas than either females in low vegetation or males in high and low vegetation, which is expected from the numerous studies that show inverse correlations between size and quality of foraging areas (see Hixon 1980). In addition, females in high vegetation showed a much greater attack response to approaching harriers than males, and females won virtually all aggressive interactions with male harriers. Finally, it is unlikely that subordinate harriers preferred to hunt in low-vegetation areas because capture success was higher there, since I found no differences in capture success between high- and low-vegetation areas.

Sexual differences in foraging behaviors.—Sexual differences in flight speeds and foraging behaviors were observed only in high-vegetation areas, where female harriers hunted by slow quartering whereas male harriers hunted by fast, straight flight. The highest hunting speeds recorded were for male harriers hunting in high vegetation, which contradicts all previous studies on the relationship between harrier hunting speeds and vegetation type (Brown and Amadon 1968, Schipper et al. 1975, Bildstein 1978). I propose that fast foraging flight was an alternative male strategy that allowed male harriers to forage in areas defended by females while minimizing detection. Ideally, this hypothesized shift should be tested by experiments in which male foraging behavior and hunting speed are examined in the absence of females (Morse 1974, Peters and Grubb 1982). However, my observations suggest that fast male flight was a behavioral shift from the slow-quartering hunting behavior usually associated with high vegetation. First, one male that entered a high-vegetation area in the absence of a defending female hunted at slow speeds (≤ 8 km/h) by quartering flight and made as many capture attempts per minute as females hunting that area. (He eventually was chased away by a female.) Second, at the beginning of the 1984 breeding season, male harriers began to attack females by chasing or hitting them (although they were unable to drive females from their foraging areas and hence "win" the interaction). Such attacks by breeding males have been observed in other avian species (Armstrong 1955, McLaren 1975). At this time, both

TABLE 8. Number of responses (e.g. attacks) to conspecifics by individual Northern Harriers per 30-min focal observation with respect to sex and vegetation height class (approached individuals only). n = sample size.

Sex	Vegetation height class	No. of responses Median	No. of responses Mean ± SD	n
Female	High	2	2.00 ± 1.15	13
	Low	1	0.86 ± 0.69	7
Male	High	0	0.00 ± 0.00	3
	Low	0	0.00 ± 0.00	4

male and female harriers hunted in high vegetation at slow speeds by quartering. Finally, no differences were observed between sexes of harriers that foraged in areas of low vegetation (see Results), yet female (but not male) hunting speeds and foraging behaviors changed in high vegetation in the manner (i.e. slow, quarter) predicted by previous studies (Brown and Amadon 1968, Schipper et al. 1975, Bildstein 1978).

Comparisons with large male–small female species.—The foraging strategies used by sexes of Northern Harriers during the nonbreeding season show striking resemblances to those of other birds, especially hummingbirds. Given that both harriers and hummingbirds are distinguished by the fact that they forage primarily on the wing, perhaps this is not surprising. Resource defense by hummingbirds is associated with differences in body weight and winglength (i.e. wing disc loading; Feinsinger and Chaplin 1975, Kodric-Brown and Brown 1978, Feinsinger et al. 1979). Heavy weight and proportionally shorter wings result in greater maneuverability, which presumably is an advantage in territorial defense by large species and the larger sex (usually males in hummingbird species weighing more than 4 g; Lasiewski and Lasiewski 1967, Carpenter 1976). The lighter weight and longer wings of smaller species and female hummingbirds result in more energetically efficient flight and hence a better ability to exploit resources, which may be important in marginal habitats or when a bird is restricted to foraging around a nest area (Kodric-Brown and Brown 1978).

In harriers, heavy weight also may be advantageous in territorial defense, but in a somewhat different way. Because terminal speed in a dive (and presumably the force of a raptor's strike) increases with increasing body mass (Andersson and Norberg 1981), weight (and overall size) may be the decisive factor in aggressive interactions between harriers, especially between males and females, where females have a size advantage (Tables 1, 2). [On this point, Marquiss and Newton (1982) commented that female Eurasian Sparrowhawks (*Accipiter nisus*) often kill and eat smaller male sparrowhawks during the nonbreeding season.] Flight costs for male harriers are much less than for female harriers, however, owing to their smaller size and lighter wing loading (Table 2). Hence, males may be better able to survive in and to exploit marginal environments.

Similarities between harriers and hummingbirds are apparent in the types of aggressive interactions between the sexes. In this study, female harriers engaged in prolonged interactions marked by much hitting, talon-clasping, and tumbling to the ground. Often an intruding female returned to a resident female's area and repeatedly harrassed her. Male harriers, on the other hand, were wary and inconspicuous. They entered a female's area quickly by flying low to the ground and fled immediately when discovered and chased by a resident female. Rapid flight is especially important if a male captures prey in a female's area: one male I observed fleeing a female's area with prey was struck by the female and had the prey snatched from him. These observations of harrier strategies correspond well to the "challenger" male (large, conspicuous, aggressive) and "robber" female (small, submissive, inconspicuous) hummingbirds discussed by Kodric-Brown and Brown (1978).

The above comparisons between harriers and hummingbirds illustrate the significance of body size in determining both the outcome of aggressive interactions and the foraging strategies of sexes of nonbreeding birds. Dominance by the larger sex may reduce food competition and may insure priority of access to preferred resources (Gauthreaux 1978, Morse 1980). However, the lower energy demands of individuals of the smaller sex may allow them to survive where larger individuals cannot (Morse 1980).

ACKNOWLEDGMENTS

I thank J. V. Remsen, Jr., and the Louisiana State University Museum of Zoology for permitting me to measure specimens of Northern Harriers in their collection. I thank T. Schoener for advice and support and D. Amadon, K. Bildstein, G. S. Mills, R. Reynolds, D. Spiller, and J. Stamps for comments on the manuscript. I especially appreciate A. Hedrick's assistance and encouragement. I thank the Davis Audubon Society, Heidrick Farms, Inc., and Hunt-Wesson Foods, Inc., for allowing me access to harrier habitat on their lands. This study was supported by Graduate Student Research Awards, Jastro-Shields Awards, and Regents' Fellowships from the University of California, Davis.

LITERATURE CITED

Altmann, J. 1974. Observational study of behaviour: sampling methods. Behaviour 79: 272–312.

Andersson, M., & R. A. Norberg. 1981. Evolution of reversed sexual dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. Biol. J. Linnaean Soc. 15: 105–130.

Armstrong, E. A. 1955. The wren. London, Collins.

Bildstein, K. L. 1978. Behavioral ecology of Red-tailed Hawks (*Buteo jamaicensis*), Rough-legged Hawks (*B. lagopus*), Northern Harriers (*Circus cyaneus*), American Kestrels (*Falco sparverius*) and other raptorial birds wintering in southcentral Ohio. Unpublished Ph.D. dissertation, Columbus, Ohio State Univ.

———, W. S. Clark, D. L. Evans, M. Field, L. Soucy, & E. Henckel. 1984. Sex and age differences in fall migration of Northern Harriers. J. Field Ornithol. 55: 143–150.

———, & M. W. Collopy. 1985. Escorting flight and agonistic interactions in wintering Northern Harriers. Condor 87: 398–401.

Boxall, P. C., & M. R. Lein. 1982. Territoriality and habitat selection of female Snowy Owls (*Nyctea scandiaca*) in winter. Can. J. Zool. 60: 2344–2350.

Brown, L., & D. Amadon. 1968. Eagles, hawks and falcons of the world. New York, McGraw-Hill.

Cade, T. J. 1955. Experiments on winter territoriality of the American Kestrel, *Falco sparverius*. Wilson Bull. 67: 5–17.

Carpenter, F. L. 1976. Ecology and evolution of an Andean hummingbird (*Oreotrochilus estrella*). Univ. California Publ. Zool. 106: 1–74.

Cramp, S., & K. E. L. Simmons. 1980. Handbook of the birds of Europe, the Middle East and north Africa, vol. II. Oxford, Oxford Univ. Press.

Daniel, W. W. 1978. Applied nonparametric statistics. Boston, Houghton Mifflin.

Evans, D. L. 1980. Vocalizations and territorial behavior of wintering Snowy Owls. Amer. Birds 34: 748–749.

Ewald, P. W., & F. L. Carpenter. 1978. Territorial responses to energy manipulations in the Anna Hummingbird. Oecologia 31: 277–292.

Feinsinger, P., & S. B. Chaplin. 1975. On the relationship between wing disc loading and foraging strategy in hummingbirds. Amer. Natur. 109: 217–224.

———, & R. K. Colwell. 1978. Community organization among nectar-feeding birds. Amer. Zool. 18: 779–795.

———, ———, J. Terborgh, & S. B. Chaplin. 1979. Elevation and the morphology, flight energetics, and foraging ecology of tropical hummingbirds. Amer. Natur. 113: 481–497.

Frost, S. K., & P. G. H. Frost. 1980. Territoriality and changes in resource use by sunbirds at *Leonotis leonurus* (Labiatae). Oecologia 45: 109–116.

Gauthreaux, S. A., Jr. 1978. The ecological significance of behavioral dominance. Pp. 17–54 *in* Perspectives in ethology, vol. 3 (P. P. G. Bateson and P. H. Klopfer, Eds.). New York, Plenum Press.

Greenewalt, C. H. 1962. Dimensional relationships for flying animals. Smithsonian Misc. Coll. No. 144(2).

Hald, A. 1952. Statistical tables and formulas. New York, John Wiley & Sons.

Hepp, G. R., & J. D. Hair. 1984. Dominance in wintering waterfowl (Anatini): effects on distribution of the sexes. Condor 86: 251–257.

Hixon, M. A. 1980. Food production and competitor density as the determinants of feeding territory size. Amer. Natur. 115: 510–530.

Hogstad, O. 1978. Sexual dimorphism in relation to winter foraging and territorial behavior of the Three-toed Woodpecker *Picoides tridactylus* and three *Dendrocopos* species. Ibis 120: 198–203.

Kilham, L. 1983. Life history studies of woodpeckers of eastern North America. Publ. Nuttall Ornithol. Club No. 20.

Kodric-Brown, A., & J. H. Brown. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. Ecology 59: 285–296.

Kuban, J. F., J. Lawley, & R. L. Neill. 1983. The partitioning of flowering century plants by Black-chinned and Lucifer hummingbirds. Southwestern Natur. 28: 143–148.

———, & R. L. Neill. 1980. Feeding ecology of hummingbirds in the highlands of the Chisos Mountains, Texas. Condor 82: 180–185.

Lasiewski, R. C., & R. J. Lasiewski. 1967. Physiological responses of the Blue-throated and Rivoli's hummingbirds. Auk 84: 34–48.

Ligon, J. D. 1968. Sexual differences in foraging behavior in two species of *Dendrocopos* woodpeckers. Auk 85: 203–215.

Marquiss, M., & I. Newton. 1982. Habitat preference in male and female Sparrowhawks *Accipiter nisus*. Ibis 124: 324–328.

Marr, T. G., & D. W. McWhirter. 1982. Differential hunting success in a group of Short-eared Owls. Wilson Bull. 94: 82–83.

McLaren, M. A. 1975. Breeding biology of the Boreal Chickadee. Wilson Bull. 87: 344–354.

MILLS, G. S. 1976. American Kestrel sex ratios and habitat separation. Auk 93: 740-748.

MORSE, D. H. 1974. Niche breadth as a function of social dominance. Amer. Natur. 108: 818-830.

———. 1980. Behavioral mechanisms in ecology. Cambridge, Massachusetts, Harvard Univ. Press.

MUELLER, H. C., D. D. BERGER, & G. ALLEZ. 1977. The periodic invasions of Goshawks. Auk 94: 652-663.

NEWTON, I. 1979. Population ecology of raptors. Vermillion, South Dakota, Buteo Books.

PENNYCUICK, C. 1972. Animal flight. London, Edward Arnold.

PETERS, W. D., & T. C. GRUBB, JR. 1982. An experimental analysis of sex-specific foraging in the Downy Woodpecker, *Picoides pubescens*. Ecology 64: 1437-1443.

POOLE, E. L. 1938. Weights and wing areas of 143 species of North American birds. Auk 55: 511-517.

PUTTICK, G. M. 1981. Sex-related differences in foraging behavior of Curlew Sandpipers. Ornis Scandinavica 12: 13-17.

SCHIPPER, W. J. A., L. S. BUURMA, & P. BOSSENBROEK. 1975. Comparative study of hunting behaviour of wintering Hen Harriers *Circus cyaneus* and Marsh Harriers *Circus aeruginosus*. Ardea 63: 1-29.

SIEGEL, S. 1956. Nonparametric statistics. New York, McGraw-Hill.

SNEDECOR, G. W., & W. G. COCHRAN. 1967. Statistical methods, 6th ed. Ames, Iowa State Univ. Press.

SNYDER, N. F. R., & H. A. SNYDER. 1970. Feeding territories in the Everglade Kite. Condor 72: 492-493.

———, & J. W. WILEY. 1976. Sexual size dimorphism of hawks and owls of North America. Ornithol. Monogr. No. 20.

STILES, F. G. 1973. Food supply and the annual cycle of the Anna Hummingbird. Univ. California Publ. Zool. 97: 1-109.

———, & L. L. WOLF. 1979. Ecology and evolution of lek mating behavior in the Long-tailed Hermit Hummingbird. Ornithol. Monogr. No. 27.

STINSON, C. H., D. L. CRAWFORD, & J. LAUTHNER. 1981. Sex differences in winter habitat of American Kestrels in Georgia. J. Field Ornithol. 52: 29-35.

TEMELES, E. J. 1985. Sexual size dimorphism of bird-eating hawks: the effect of prey vulnerability. Amer. Natur. 125: 485-499.

WOLF, L. L., F. G. STILES, & F. R. HAINSWORTH. 1976. Ecological organization of a tropical, highland hummingbird community. J. Anim. Ecol. 45: 349-379.

"Federal Wildlife Permit Procedures" (vol. 1 of "Controlled Wildlife"), compiled by Carol Estes and Keith W. Sessions, is now available. It is a comprehensive guide to the labyrinth of federal statutes relating to wildlife. Includes descriptions of the various procedures involved in obtaining and transporting wildlife and for dealing with bird specimens (living or dead). Available for **$55.00** from: **Association of Systematic Collections, Museum of Natural History, University of Kansas, Lawrence, Kansas 66045.**

DISPERSAL IN WHITE-CROWNED SPARROWS: A COMPUTER SIMULATION OF THE EFFECT OF STUDY-AREA SIZE ON ESTIMATES OF LOCAL RECRUITMENT

MICHAEL A. CUNNINGHAM[1]
Department of Zoology and Entomology, Colorado State University,
Fort Collins, Colorado 80523 USA

ABSTRACT.—Consideration of the problem of sampling a population within a finite study area suggested that recruitment results might be related to the size of the study area. Specifically, the proportion of recruits observed within a defined study area that originate in that area (local recruits) should be a function of the proportion of the population that the study area represents. Computer simulations of dispersal, using Nuttall's White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*) as a model, were designed to test this hypothesis, and the effect of territory size and population size on this relationship. The simulations confirmed that local recruitment is a function of the proportion of the population sampled in the study area. Additionally, these simulations demonstrated that by holding the distribution of dispersal distances constant, local recruitment for a given proportion of the population sampled increased with territory size and population size. These latter results, however, are artifacts of the simulations and have no biological significance. Finally, the proportion of local recruits predicted for a natural population was remarkably close to that obtained from fieldwork. I suggest that conclusions about dispersal and population structure should not be drawn from proportions of local recruitment within finite study areas, and require more detailed analysis of dispersal. *Received 7 December 1984, accepted 11 July 1985.*

ANALYSES of dispersal (Howard 1960), and the attendant gene flow (Wright 1940, 1943, 1946, 1951; Murray 1967; Crumpacker and Williams 1973; Powell et al. 1976; Endler 1977), are important to understanding population structure and evolutionary processes (Barrowclough 1978, Greenwood and Harvey 1982, Shields 1982). Conclusions about dispersal are often not derived from observed zygote-to-zygote dispersal distances. Instead, a study area is defined within a population and an attempt is made to mark all individuals produced within that study area. In subsequent breeding seasons, the study area is censused to determine what proportion of the breeding adults originated within the study area. From such "local turnover," inferences are drawn about the magnitude of dispersal among study populations (Petrinovich et al. 1981). Petrinovich and Patterson's work (1982; see also Baptista and Morton 1982) on the stability, recruitment, and population structure of Nuttall's White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) is an example of this latter approach.

Estimating dispersal from local turnover has an inherent problem: the proportion of "local" recruits (i.e. those produced within the study area) is related to the proportion of the breeding population sampled in the study area. Consider a small hypothetical study area including only a single territory, and a dispersal rule that individuals cannot settle within their natal territory. Clearly, the proportion of recruits to the study area that originated there (local recruits) will be zero. At the other extreme, a study area encompassing the entire breeding population will necessarily contain 100% local recruits. Most study areas lie somewhere between these extremes, representing some portion of the population of interest.

To demonstrate the relationship between local recruitment and the proportion of a population sampled, I designed a computer simulation of dispersal and sampled defined study areas. To make this simulation representative of a natural population, I drew the necessary parameters from the literature on the demog-

---

[1] Present address: Department of Zoology, Ohio State University, Lima Regional Campus, 4240 Campus Drive, Lima, Ohio 45804 USA.

raphy and dispersal of Nuttall's White-crowned Sparrow. The general conclusions from this analysis should, however, be applicable to essentially any population of dispersing organisms. Finally, I simulated Petrinovich and Patterson's (1982) study conditions to see if the proportion of local recruits predicted from my model would be comparable to their empirical result.

COMPUTER SIMULATIONS

Simulations were programmed in Applesoft BASIC on an Apple II+ computer. The first simulation was designed to determine the relationship between local recruitment and the proportion of a population sampled, and to determine the effect of territory size on that relationship, for a given dispersal distribution. The population was defined as a square array of 625 territories, 25 on a side. This approximates the size of a song dialect population at Point Reyes National Seashore, California (300-800 pairs/dialect, Baker 1981; pers. obs.). The population was stored in computer memory as a two-dimensional array and treated as a hexagonal array by manipulation of the addresses (Page and Didday 1980). The advantage of the hexagonal arrangement was that each territory (with the exception of boundary territories) was surrounded by six neighboring territories whose centers were equidistant from the center of the territory they bounded. In nature, the spatial arrangement of territories may be highly variable, but an approximation to hexagonal packing is common (Nice 1937, Lack 1966, Leuthold 1966, Grant 1968, Southern 1970, Barlow 1974, Wilson 1975, Ligon and Ligon 1982). Study areas were defined as square arrays centered within the population and represented samples of the population ranging from approximately 5% to 95% at approximately 5% intervals.

Each simulation began by establishing the status of all territories within the population. A survivorship test determined whether each territory was occupied by a surviving adult or was available to a recruit. Survivorship was 50% for each adult generation (Mewaldt 1964, Baker et al. 1981). For simplicity, each territory was occupied by a single individual rather than a pair [simulating pairs would have required running the program twice (once for each sex, assuming the sexes disperse independently) and averaging the results to obtain a single proportion], and recruitment was limited to first-year birds, i.e. adult movement was not considered.

Dispersal began by randomly selecting a territory of origin from the entire population, then determining a target territory by randomly generating a dispersal direction and distance. Dispersal directions were chosen randomly to be along one of the six axes through the six neighboring territories. Dispersal distances were selected probabilistically from a two-parameter gamma distribution fitted by Baker and Mewaldt (1978) to dispersal data for both sexes from White-crowned Sparrow populations at Point Reyes, California. For this distribution, gamma = 0.89352 and the two parameters were calculated to be alpha (α) = 0.6 and beta (β) = 366.8. Alpha is a shape parameter and beta is a scale parameter, where the mode = $\alpha\beta$ and the mean = $(\alpha + 1)\beta$ (Johnson and Kotz 1970, Hastings and Peacock 1975). Dispersal distances were calculated in meters and converted into territorial units by dividing that distance by the territorial diameter. Hexagonal polygons have two diameters, side-to-side (minimum) and corner-to-corner (maximum). All simulations in this study used minimum diameters for territory diameters.

Dispersing individuals were moved to the target territory, determined by the dispersal direction and distance, using the hex address manipulation. If the territory was available (not occupied by a surviving adult or previously dispersed juvenile), the dispersing juvenile occupied that territory; if the territory was occupied, the dispersing juvenile searched the six neighboring territories and occupied the first available territory encountered. Once the dispersing juvenile settled, it was noted whether it had originated from within or from outside the study area. Following this, or if the disperser was not able to settle in the target territory or one of the six neighboring territories, a new territory of origin was randomly selected and dispersal of a new individual was initiated in like manner. The populations defined in these simulations were finite, and the boundaries were absorbing; i.e. if a dispersing juvenile contacted a boundary he was eliminated, and dispersal of a new juvenile was initiated. The number of juveniles that could disperse from a given territory was not limited (White-crowned Sparrows may produce more than one clutch/season with up to 4-5 young/clutch), but on each iteration the territory of origin was again chosen randomly. Dispersal iterations continued until all territories within the study area were occupied. The study area was then censused to determine the proportion of recruits that originated within the study area.

This simulation used four different territory diameters (20, 40, 80, and 160 m) and 16 study-area proportions (from about 6% to 92% at approximately 5% intervals). The simulation was repeated 20 times for each of the combinations of territory diameter and study-area proportion. This range of territory diameters was chosen because it brackets those reported for Nuttall's White-crowned Sparrow. The smallest territories were reported in San Francisco and averaged 1,127 m^2 (Patterson and Petrinovich 1978, Petrinovich and Patterson 1982). The minimum diameter of hexagonal territories of this area would be

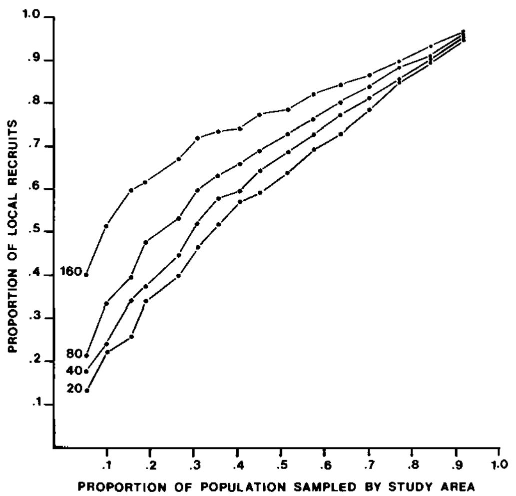

Fig. 1. Proportion of local recruits as a function of the proportion of the population sampled in the study area. Each curve represents the plotted means of 20 runs for each of 16 study-area proportions, for territory diameters of 20, 40, 80, and 160 m. The population size was 625 territories, and the dispersal parameters were: alpha = 0.6, beta = 366.8, and gamma = 0.89352.

approximately 36 m. The average territories at Point Reyes range in size from 2,360 m^2 (Ralph and Pearson 1971) to 4,452 m^2 (Chamberlain 1972). These figures produce minimum diameters of hexagonal territories in the range of 52–72 m.

A second simulation was performed to compare the proportion of local recruits predicted from my model with an empirical result (Petrinovich and Patterson 1982). The Presidio study area of Petrinovich and Patterson represented approximately 15% of the Presidio dialect area (as determined by measurements taken from Fig. 1 of Petrinovich and Patterson 1982) and contained about 31 territories. Assuming the population density of the entire dialect area was the same as in the study area, the population of the Presidio dialect included about 203 territorial pairs. For the purpose of simulation, the nearest square array of territories, representing the Presidio dialect population, is a 14 × 14 array of 196 territories. Because Petrinovich and Patterson did not provide a dispersal distribution for their study population, I assumed dispersal followed that reported by Baker and Mewaldt (1978). I used 40 m as the territory diameter because it approximated the diameter of a Presidio territory (for a hexagonal territory of 1,127 m^2, min. diam. = 36.1, max. diam. = 41.7). The simulation was repeated 20 times for each of 11 study-area proportions (from about 5% to 86% at approximately 5–10% intervals). Finally, by comparison with the results from the previous simulation, which used the same dispersal distribution and territory diameter, I was also able to determine the effect of population size on the proportion of local recruits observed within a study area.

TABLE 1. Power-curve regression coefficients for dispersal simulations.[a]

Population size (territories)	Territory diameter	Median territories dispersed	*a*	*b*
625	20	18.75	1.0156	0.6942
625	40	9.38	1.0175	0.6090
625	80	4.69	1.0220	0.5082
625	160	2.34	0.9797	0.2932
196[b]	40	9.38	1.1349	0.8432

[a] Power function: $y = ax^b$; median dispersal distance = 375 m; dispersal parameters: alpha = 0.60, beta = 366.8, gamma = 0.89352.

[b] Simulation comparable to the field study by Petrinovich and Patterson (1982).

RESULTS AND DISCUSSION

Two clear relationships emerged from the first simulation. First, the proportion of local recruits is an increasing function of the proportion of the breeding population that the study area encompasses (Fig. 1). The shape of these curves suggests a simple power function of the form: $y = ax^b$, where a and b are constants. Theoretically, for this particular problem, y (the proportion of local recruits) should equal 1.0 when x (the proportion of the population sampled in the study area) is 1.0. The simulation confirms this (Fig. 1). Thus, the constant a should equal 1.0, and the power function reduces to $y = x^b$. Within the range of parameters used in this simulation, the exponent b should assume some value between 0.0 and 1.0. For each of the four territory diameters used in this simulation, I fitted power curves to the mean values of the 20 runs for each study-area proportion, and the theoretical point of x = 1.0, y = 1.0. The theoretical point of x = 0.0, y = 0.0 could not be included because of logarithms in the curve-fitting program. In all four cases the coefficient a was within 3% of the expected value of 1.0 (Table 1).

The second relationship suggested by this simulation is that for a given distribution of dispersal distances and a given proportion of

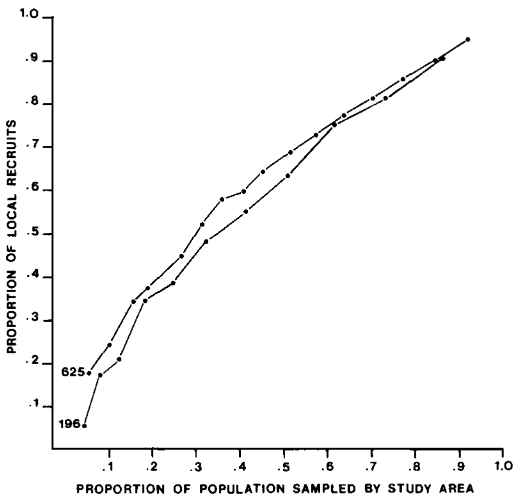

Fig. 2. Proportion of local recruits as a function of the proportion of the population sampled in the study area. The curves represent the plotted means of 20 runs for each of 16 (upper curve) and 11 (lower curve) study-area proportions, for populations of 625 (upper curve) and 196 (lower curve) territories. The territory diameter was 40 m, and the dispersal parameters were: alpha = 0.6, beta = 366.8, and gamma = 0.89352. The upper curve is from the first simulation and is also shown in Fig. 1.

the population sampled in the study area, the proportion of local recruits increases with increasing territory diameter (Fig. 1). That is, for a given distribution of absolute dispersal distances, as the territory diameter increases, the number of territories dispersed decreases (Table 1). The second simulation, with dispersal distribution and territory diameter held constant, indicated that, for a given proportion of the population sampled, the proportion of local recruits increased as the size of the population increased (Fig. 2). Both of these results are purely artifacts of the simulations, and for the same reason. As the area occupied by a population increases, either because territory size or population size increases, the study area must likewise increase to sample the same proportion of the population. If the dispersal distribution remains constant and the study-area size is increased, then fewer of the individuals produced within the study area disperse beyond its boundaries. It is important to keep these relationships in mind when considering these simulations, as they influence the absolute values of the dependent variable (proportion of local recruits), but they should not change the general trends in the relationships described here.

The result of decreasing dispersal (higher local recruitment) with increasing territory size (Fig. 1), in addition to being an artifact of the simulation, probably does not apply to natural populations. Dispersal is a discrete rather than a continuous process because territorial species disperse from territory to territory and not simply absolute distances (Shields 1982). In natural populations, we would expect that as territory size increases so will absolute dispersal distances, because individuals are forced to move longer distances while crossing the same number of territories. With regard to population size, Nuttall's White-crowned Sparrow presents some special problems because this subspecies is subdivided by song dialects. In this study I assumed that song dialects represent distinct populations; however, this has been a point of some debate (for review see Baker and Cunningham 1985). If song dialects are not (relatively) distinct populations, the actual population size would be much larger. This would change the position of the recruitment curve, as demonstrated by the second simulation (Fig. 2). In natural populations the dispersal distribution itself is an important determinant of the "effective" population size (Wright 1943, 1951; Baker 1981); for dialect species, such as the White-crowned Sparrow, the effective population size will depend upon both the dispersal distribution and the effect of dialect boundaries (Baker and Mewaldt 1978, Baker 1981).

The more important objective of the second simulation was to compare the proportion of local recruits predicted from the model with that observed previously (Petrinovich and Patterson 1982). Petrinovich and Patterson reported that only 16% of all recruits were produced within their study areas. Elsewhere (Petrinovich et al. 1981) they concluded, from this low proportion of local recruits, that there must be significant cross-dialect dispersal. They counted adults that moved into their study areas as recruits, as well as first-year birds. In my simulations, I considered only juveniles as recruits. For comparison I used only the first-year birds (nestlings, fledglings, and first-year brown crowns) from Petrinovich and Patterson's (1982) data. Of the 182 first-year birds that settled in their study areas, 51 had been banded there as nestlings, giving a local recruitment of 28%. These recruitment figures are combined data from two study sites, the Presidio and Twin Peaks, but the authors stated that the data were treated separately only in those instances in which the results were different for the two study areas. I assumed that the data from the Presidio and Twin Peaks were similar. It is difficult to determine what proportion of the San Francisco dialect population the Twin Peaks study area represented, because the San Francisco dialect population is highly fragmented in an urban area, and the full extent of the dialect is not shown on the map provided (Petrinovich and Patterson 1982). However, the Presidio dialect area is indicated (see also Petrinovich et al. 1981), and the Presidio study area represented about 15% of the dialect area.

The results of the second simulation are plotted in Fig. 2 (lower curve), and the power-curve regression coefficients are given in Table 1. This regression was not as close to the theoretical asymptote, where the coefficient $a = 1.0$, as the regressions in the previous simulation (Table 1). Using the simplified power function, $y = x^b$, the predicted proportion of local recruits was 20% for a study area containing 15% of the population, but this curve did not fit the data well and yielded predicted values almost 12% below that of the fitted power curve. The power function using the calculated coefficient (a) of 0.1349 provided a better fit than the simplified function, but the fit still was not good because it predicted values less than the observed means for x in the range of 8-41% and greater than the observed means for x in the range of 51-100%. Using this fitted power curve, the predicted value for a study area containing 15% of the population was 23%. The observed means (from 20 computer runs) for study areas containing 13% and 18% of the population were 21% and 35%, respectively. Linear interpolation between these values for a study area containing 15% of the population yields 27% local recruits.

All three of the predicted values for the proportion of local recruits, from a study area containing about 15% of a population of 196 territories, were close to the 28% local recruits observed by Petrinovich and Patterson (1982), the third being remarkably close. This close correspondence between observed values of local recruitment and those predicted by my model suggests that there may be nothing surprising about the findings of Petrinovich and Patterson, and inferences about interdialect exchange made from these data (Petrinovich et al. 1981) might be invalid. In fact, neither these simulations nor the results of Petrinovich and Patterson directly address the issue of interdialect dispersal. Some qualifications are in order because there are a number of complicating factors that render this simulation only an approximation of the population that Petrinovich and Patterson studied.

Because of the lack of detailed dispersal data from the Presidio population, I used the dispersal distribution parameters from the Point Reyes populations (Baker and Mewaldt 1978). This distribution is given in absolute distances rather than number of territories moved. The territories at the Presidio tend to be only 25-50% as large as those at Point Reyes. If birds disperse by territorial units rather than by absolute distance (Shields 1982), and if dispersal is similar at the Presidio and Point Reyes, then the dispersal distances should be proportionately shorter for the Presidio population. A distribution of shorter dispersal distances should increase the proportion of local recruits for a given-size study area.

The physical habitat at the Presidio is quite different from that at Point Reyes (Baker and Mewaldt 1981; pers. obs.). In the Presidio, suitable breeding habitat is patchy, crossed by major highways, and fully within an urban area, while Point Reyes provides larger tracts of continuous breeding habitat in a natural "wilderness" area. Thus, birds at the Presidio commonly may have to disperse across areas of unsuitable habitat before locating an available territory. A patchy distribution of breeding habitat would tend to increase the absolute dispersal distances, thus decreasing the proportion of local recruits, perhaps counteracting the effect of smaller territory size.

The results of my simulations support the argument that the proportion of local recruits observed within a study area depends on the proportion of the breeding population encompassed by that study area. This relationship can be described by a simple power function. While my simulation only roughly approximates the conditions at the Presidio, it suggests that the proportion of local recruits observed there might not be unexpectedly small; it does not necessarily indicate that "a sizable proportion of banded nestlings dispersed out of the Presidio" (Petrinovich et al. 1981). In fact, the proportion of local recruits observed within a study area is a function of the size of the study area in relation to the dispersal distribution itself, which is the important determinant of the "effective" population size. Reliable conclusions about dispersal and population structure cannot be made from proportions of local recruitment in finite study areas. To evaluate the structure of natural populations, detailed analyses of dispersal are needed that consider the territorial nature of the population, the effects of social interactions (e.g. dialect effects), and the distribution of suitable habitat.

ACKNOWLEDGMENTS

I acknowledge L. Petrinovich and T. L. Patterson, whose work was the stimulus for this analysis. While I have been critical of their interpretations, I admire the important empirical contribution of their extensive work. I am grateful to M. C. Baker, C. R. Tracy, R. M. Casey, and W. M. Shields for reading and commenting on this paper. I am especially grateful to M. C. Baker and C. R. Tracy for their advice and encouragement, and to C. R. Tracy for allowing me to pursue this exercise in partial fulfillment of the Ph.D. preliminary examination requirement at Colorado State University. Finally, I would like to express my appreciation to L. Petrinovich and D. DeSante for their helpful reviews of this paper.

LITERATURE CITED

BAKER, M. C. 1981. Effective population size in a songbird: some possible implications. Heredity 46: 209-218.

———, & M. A. CUNNINGHAM. 1985. The biology of bird song dialects. Behav. Brain Sci. 8: 85-133.

———, & L. R. MEWALDT. 1978. Song dialects as barriers to dispersal in White-crowned Sparrows, *Zonotrichia leucophrys nuttalli*. Evolution 32: 712-722.

———, & ———. 1981. Response to "Song dialects as barriers to dispersal: a re-evaluation." Evolution 35: 189-190.

———, ———, & R. M. STEWART. 1981. Demography of White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*). Ecology 62: 636-644.

BAPTISTA, L. F., & M. L. MORTON. 1982. Song dialects and mate selection in montane White-crowned Sparrows. Auk 99: 537-547.

BARLOW, G. W. 1974. Hexagonal territories. Anim. Behav. 22: 876-878.

BARROWCLOUGH, G. F. 1978. Sampling bias in dispersal studies based on finite area. Bird-Banding 49: 333-341.

CHAMBERLAIN, B. 1972. Observations of breeding White-crowned Sparrows. Point Reyes Bird Obs. Newsletter No. 23.

CRUMPACKER, D. W., & J. S. WILLIAMS. 1973. Density, dispersion, and population structure in *Drosophila pseudoobscura*. Ecol. Monogr. 43: 499-538.

ENDLER, J. A. 1977. Geographic variation, speciation, and clines. Princeton, New Jersey, Princeton Univ. Press.

GRANT, P. R. 1968. Polyhedral territories of animals. Amer. Natur. 102: 75-80.

GREENWOOD, P. J., & P. H. HARVEY. 1982. The natal and breeding dispersal of birds. Ann. Rev. Ecol. Syst. 13: 1-21.

HASTINGS, N. A. J., & J. B. PEACOCK. 1975. Statistical distributions. New York, Halstead Press, John Wiley & Sons.

HOWARD, W. E. 1960. Innate and environmental dispersal of individual vertebrates. Amer. Midl. Natur. 63: 152-161.

JOHNSON, N. L., & S. KOTZ. 1970. Distributions in statistics: continuous univariate distributions—1. Boston, Houghton Mifflin.

LACK, D. 1966. Population studies of birds. Oxford, Oxford Univ. Press.

LEUTHOLD, W. 1966. Territorial behavior of Uganda kob. Behaviour 27: 255-256.

LIGON, D. J., & S. H. LIGON. 1982. The cooperative breeding behavior of the Green Woodhoopoe. Sci. Amer. 247: 126-134.

MEWALDT, L. R. 1964. Effects of bird removal on a winter population of sparrows. Bird-Banding 35: 184-195.

MURRAY, B. G. 1967. Dispersal in vertebrates. Ecology 48: 975-978.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow. Trans. Linnaean Soc. New York 4: 1-247.

PAGE, R., & R. DIDDAY. 1980. Fortran 77 for humans. St. Paul, Minnesota, West Publ. Co.

PATTERSON, T. L., & L. PETRINOVICH. 1978. Territory size in the White-crowned Sparrow (*Zonotrichia leucophrys*): measurement and stability. Condor 80: 97-98.

PETRINOVICH, L., & T. L. PATTERSON. 1982. The White-crowned Sparrow: stability, recruitment, and population structure in the Nuttall subspecies (1975-1980). Auk 99: 1-14.

———, ———, & L. F. BAPTISTA. 1981. Song dialects as barriers to dispersal: a re-evaluation. Evolution 35: 180-188.

POWELL, J. R., T. DOBZHANSKY, J. E. HOOK, & H. E. WISTRAND. 1976. Genetics of natural populations. XLIII. Further studies on rates of dispersal of *Drosophila pseudoobscura* and its relatives. Genetics 82: 493-506.

RALPH, C. J., & C. A. PEARSON. 1971. Correlation of age, size of territory, plumage, and breeding success in White-crowned Sparrows. Condor 73: 77-80.

SHIELDS, W. M. 1982. Philopatry, inbreeding, and the evolution of sex. Albany, State Univ. New York Press.

SOUTHERN, H. N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). J. Zool. London 162: 197-285.

WILSON, E. O. 1975. Sociobiology, the new synthesis. Cambridge, Massachusetts, Harvard Univ. Press.

WRIGHT, S. 1940. Breeding structure of populations in relation to speciation. Amer. Natur. 74: 232-248.

———. 1943. Isolation by distance. Genetics 28: 114-138.

———. 1946. Isolation by distance under diverse systems of mating. Genetics 31: 39-59.

———. 1951. The genetical structure of populations. Ann. Eugenics 15: 323-354.

Repository for Voucher Photographs at VIREO

Photographs to document critical aspects of research methods and results in papers published in *The Auk* can be deposited with Visual Resources for Ornithology (VIREO) for long-term archival care. VIREO accession numbers for these photographs can then be published to enable subsequent access to the photographs for comparison, research, and teaching.

Voucher photographs should document critical and unique features of the published work, and normally should *not* be photographs published with the paper. Photographs of habitat and study-site slides are of exceptional importance for ecological and behavioral studies. Specific plumages, soft-body part colors, or morphological characters central to methods and results also would be appropriate, as would photographs illustrating novel techniques.

Preferably, authors will deposit original photographs with VIREO; if needed, a reproduction-quality duplicate is then returned. If the photographer must retain the original, then VIREO will place a reproduction-quality duplicate in archival storage. In this case VIREO requires temporary access to the original for duplication.

Authors interested in using this service should contact VIREO immediately after being notified of the acceptance of their papers for publication in *The Auk*: **VIREO, Academy of Natural Sciences, 19th and the Parkway, Philadelphia, Pennsylvania 19103 USA** (215-299-1069).

B., J. J. Reyes R., Wilfrido Contreras D.) of Dirección General de la Fauna Silvestre, Secretaría de Agricultura y Recursos Hidráulicos (México, D.F.). Officials of the Mérida office of División Hidrométrica, SARH, kindly gave us access to weather data. George and Janet Cobb, Joann Andrews, and Edward Kurjack were generous hosts in Yucatán. We thank Anne Clark, Paul Mason, and two anonymous reviewers for useful criticisms of a draft of this paper. Partial support for this study was provided by The Explorers Club and by the Texas Memorial Museum-The University of Texas at Austin. The Museum of Zoology of Louisiana State University provided computer time.

LITERATURE CITED

CLARK, A. B., & D. S. WILSON. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. Quart. Rev. Biol. 56: 253-277.

CONOVER, W. J. 1980. Practical non-parametric statistics. New York, John Wiley & Sons.

KOENIG, W. D. 1982. Ecological and social factors affecting hatchability of eggs. Auk 99: 526-536.

LACK, D. 1947. The significance of clutch size. Ibis 89: 302-352.

MARTIN, M. W., & R. F. MARTIN. 1985. Nestling feeding schedules of Turquoise-browed Motmots in Yucatán, Mexico. Wilson Bull. 97: 372-374.

OREJUELA, J. E. 1977. Comparative biology of Turquoise-browed and Blue-crowned motmots in the Yucatan Peninsula, Mexico. Living Bird 16: 193-208.

SCHREIBER, R. W., & E. A. SCHREIBER. 1983. The world according to El Niño. Abstr., 101st stated meeting of Amer. Ornithol. Union, New York.

SCOTT, P. E. 1984. Reproduction of the Turquoise-browed Motmot in Yucatán, Mexico. Unpublished M.A. thesis, Austin, Univ. Texas.

———, & R. F. MARTIN. 1983. Reproduction of the Turquoise-browed Motmot at archaeological ruins in Yucatán. Biotropica 15: 8-14.

The **Frank M. Chapman Memorial Fund** gives grants in aid of ornithological research and also postdoctoral fellowships. While there is no restriction on who may apply, the Committee particularly welcomes and favors applications from graduate students; projects in game management and the medical sciences are seldom funded. **Applications are reviewed once a year and should be submitted no later than 15 January—with all supporting material.** Application forms may be obtained from the **Frank M. Chapman Memorial Fund Committee, % Jane Connelly, The American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192.**

Dr. Mary McKitrick was appointed Chapman Fellow for the period May 1985 through May 1986. She is studying the significance of individual variation in M. flexor cruris lateralis in the Tyrannidae.

Dr. Nina Pierpont was appointed Chapman Fellow for the period October 1985 through October 1986. She is studying the evolution of diversity in woodcreepers (Aves: Dendrocolaptidae).

Chapman grants during 1985, totalling $25,482 with a mean of $499.65, were awarded to: David J. Anderson, booby breeding and feeding and marine resources in the Galapagos; John Anderson, tests of cooperative foraging in the White Pelican; Dr. Bonnie Bowen, genetic structure and paternity in communally breeding jays; Angelo Capparella, effects of riverine barriers on gene flow in Amazonian forest undergrowth birds; William J. Carmen, social behavior and ecology of the California Scrub Jay; Richard Casey, the effect of social interaction during the critical period of song learning in White-crowned Sparrows; Peng Chai, avian feeding behavior and its implications for the evolution of neotropical butterfly mimicry; Jack Clinton-Eitniear, *Cathartes burrovianus*: movement patterns and systematics; Nonie Coulthard, the White-throated Bee-eater (*Merops albicollis*): a study of cooperative breeding in relation to ecological factors; Marilyn England, breeding biology of the Northern Harrier on Long Island, New York; Christian Erard, systematics of African Muscicapidae; Mark A. Finke, male parental care and the evolution of reproductive effort: an experimental test; Dr. Jon Fjeldsa, museum work for a field guide and biogeographic analysis of the Andean avifauna; Ronald C. Gaines, nest site tenacity and philopatry of the Ferruginous Hawk; Steven M. Goodman, museum tour for the birds of Egypt and project; Frederick P. Greene, determinants of guild structure among insectivorous birds; Jeffrey G. Groth, systematics of the Red Crossbill in western North America, using vocal, morphological and electrophoretic data; John M. Hagan, colonial nesting in Ospreys; Dionyssia Hatzilacos, breeding and feeding biology of the White Pelican (*Pelecanus onocrotalus*) nesting at Lake Mikra Prespa—measures for protection; P. Hibbard, John P. Dunning, Laurie M. McKean, and Richard Bowers, the efficiency of foraging behavior: an experimental approach; Geoffrey E. Hill, the reproductive consequences of sub-adult plumage

(*continued on p. 22*)

for at least 30 days. Adult Leach's Storm-Petrels, fish, shellfish, crabs, and chickens were the main food items. The following equation was used to determine the total wet weight of the *i*th food: $W_i = (D_i \times R_i \times TER)/(\Sigma D_iR_iC_i)$, where D_i = dry weight of the *i*th food, R_i = regurgitation coefficient of the *i*th food (showing the ratio between wet weight of intake and dry weight of pellets), TER = total energy requirement of the gulls for 5 days, and C_i = caloric value of the *i*th food. C_is (kcal/kg wet weight) were assumed to be the following: adult Leach's Storm-Petrel, 2,600; fish, 1,500; crab with shell, 700; shellfish with shell, 500; chicken, 3,000 (Brisbin 1968, Hunt 1972, Sibly and McCleery 1983). R_is were assumed to be the same as those of Black-tailed Gulls (*Larus crassirostris*) and the following: adult Leach's Storm-Petrel, 5.9; fish, 317.3; crab, 6.7; shellfish, 2.2; chicken, 30.0 (Watanuki 1984). The number of petrels killed by gulls was calculated by dividing the total petrel wet weight by the average individual adult weight (48 g, Watanuki 1985b). Seasonal changes in the gulls' diet composition are shown in Fig. 7.

(*continued from p. 13*)

in male Black-headed Grosbeaks; Adan (Hussein) Isack, biology of the Greater Honeyguide (*Indicator indicator*); Dr. Pedro Jordano, pattern of fruit use by wintering frugivorous birds and their implications for bird-dispersed plants in Mediterranean habitats; Frank J. Joyce, nest site selection by three passerine associates of Hymenoptera; Donald M. Kent, foraging strategies of Snowy Egrets (*Egretta thula*) in the salt marshes of Massachusetts; Roni King, winter territoriality in migratory European Robins (*Erithacus rubecula*)—habitat selection and winter survivorship; Francis R. Lambert, co-adaptation between frugivorous birds and fig trees in Malaysian lowland forest; Jeanette L. Lebell, microgeographic variation in the flight whistle of the Brown-headed Cowbird; David E. Manry, a preliminary study of blood and feather pulp proteins in two South American ibis (Threskiornithidae) species; Jean-Louis Martin, the population structure of *Parus caeruleus* L. (Aves): geographical variation and speciation in the Mediterranean region; Jon Miller, breeding distribution and origin of Water Pipits in the Sierra Nevada; David Morimoto, effects of forest fragmentation on avian community structure and species-habitat relationships in the southeastern Massachusetts Pine Barrens; Jay Pitocchelli, speciation in the genus *Oporornis*; Richard O. Prum, courtship behavior and ecology of *Masius chrysopterus* in Ecuador; Dr. Michael R. W. Rands, the breeding behavior and habitat of the Arabian Bustard, *Ardeotis arabs*; Pamela C. Rasmussen, relationships of Fuego-Patagonian Blue-eyed Shags; Mark D. Reynolds, social behavior of Yellow-billed Magpies; Dr. Gary Ritchison, the significance of song repertoires in the Northern Cardinal; Jeffrey A. Schwartz, vocal similarity in mated Ring-billed Gulls as an aid in parental recognition by young; Dr. Ron Scogin, floral color and hummingbird vision; Peter E. Scott, the nesting ecology of desert hummingbirds in relation to the pollination ecology of certain nectar plants; Patricia Serrentino, the breeding ecology and behavior of the Northern Harrier (*Circus cyaneus*) in Coos County, New Hampshire; Laurie J. Stuart-Simons, food limitation in birds; Richard R. Snell, hybridization, isolation and species recognition in arctic gulls; Carol Spaw, thick-shelled eggs and their evolutionary implications; Charles Sullivan, nest behavior and development of young in the Jabiru Stork; Dr. Kimberly A. Sullivan, energetics and the development of time-budgeting; Richard John Watling, investigation of status of Ogea Flycatcher and Blue-crowned Lory; Dr. G. Causey Whittow, water loss from eggs of Great Frigatebird (*Fregata minor*); Dr. David Winkler, a general model of parental care with experimental tests on the Tree Swallow; John L. Zimmerman, *Ortstreue* in Henslow's Sparrows (*Ammodramus henslowii*) and movements in response to spring burning of tallgrass prairie.

DOWLING, T. E., & W. S. MOORE. 1984. Level of reproductive isolation between two cyprinid fishes, *Notropis cornutus* and *N. chrysocephalus*. Copeia 1984: 617-628.

———, & ———. 1985. Evidence for selection against hybrids in the family Cyprinidae (genus *Notropis*). Evolution 39: 152-158.

GILL, F. B. 1980. Historical aspects of hybridization between Blue-winged and Golden-winged warblers. Auk 97: 1-18.

JOHNSON, N. K., & C. B. JOHNSON. 1985. Speciation in sapsuckers (*Sphyrapicus*): II. Sympatry, hybridization, and mate preference in *S. ruber daggetti* and *S. nuchalis*. Auk 102: 1-15.

KOENIG, W. D. 1982. Ecological and social factors affecting hatchability of eggs. Auk 99: 526-536.

———. 1984. Geographic variation in clutch size in the Northern Flicker (*Colaptes auratus*): support for Ashmole's hypothesis. Auk 101: 698-706.

LEHRMAN, D. S. 1965. Interaction between internal and external environments in the regulation of the reproductive cycle of the Ring Dove. Pp. 355-380 *in* Sex and behavior (F. A. Beach, Ed.). New York, John Wiley & Sons.

MOORE, W. S. 1977. An evaluation of narrow hybrid zones in vertebrates. Quart. Rev. Biol. 52: 263-277.

———, & D. B. BUCHANAN. 1985. Stability of the Northern Flicker hybrid zone in historical times: implications for adaptive speciation theory. Evolution 39: 135-151.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, & D. H. BENT. 1975. SPSS, statistical package for the social sciences, 2nd ed. New York, McGraw-Hill.

REMINGTON, C. L. 1968. Suture-zones of hybrid interaction between recently joined biotas. Pp. 321-428 *in* Evolutionary biology, vol. 2 (T. Dobzhansky, M. K. Hecht, and W. C. Steere, Eds.). New York, Appleton-Century-Crofts.

RICKLEFS, R. E. 1980. Geographic variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97: 38-49.

RISING, J. D. 1983a. The Great Plains hybrid zones. Pp. 131-157 *in* Current ornithology, vol. 1 (R. F. Johnston, Ed.). New York, Plenum Publ. Corp.

———. 1983b. The progress of oriole hybridization in Kansas, USA. Auk 100: 885-897.

SHERMAN, A. R. 1910. At the sign of the Northern Flicker. Wilson Bull. 22: 133-171.

SHORT, L. L. 1965. Hybridization in the flickers (*Colaptes*) of North America. Bull. Amer. Mus. Nat. Hist. 129: 307-428.

———. 1969. Taxonomic aspects of avian hybridization. Auk 86: 84-105.

———. 1970. A reply to Uzzell and Ashmole. Syst. Zool. 19: 199-201.

THORNTHWAITE ASSOCIATES. 1964. Average climatic water balance data of the continents, part VII. Lab. Climatol. Publ. Climatol. 17: 419-615.

WILSON, E. O. 1965. The challenge from related species. Pp. 7-25 *in* The genetics of colonizing species (H. G. Baker and G. L. Stebbins, Eds.). New York, Academic Press.

The American Ornithologists' Union solicits nominations for its **Brewster and Coues Awards.** Nominations and supporting materials should be sent to **Dr. Elsie C. Collias, Department of Biology, University of California, Los Angeles, California 90024.** Materials must be received before **1 March 1986.**

Wisconsin Project Loon Watch is accepting applications for its first annual **Sigurd T. Olson Common Loon Research Award** for research on Common Loons in the Lake Superior-Lake Michigan region of the United States and Canada. To apply, submit a brief (maximum 10 pages) description of the proposed research program and curriculum vitae to **Dr. Paul I. V. Strong, Director, Wisconsin Project Loon Watch, Sigurd Olson Environmental Institute, Northland College, Ashland, Wisconsin 54806 USA** no later than **1 March 1986.** Proposals by students should be accompanied by two letters of recommendation. The $1,000 award will be granted on the basis of the project's potential to better understand and manage Upper Great Lakes populations of Common Loons.

Mills, G. S. 1976. American Kestrel sex ratios and habitat separation. Auk 93: 740-748.

Morse, D. H. 1974. Niche breadth as a function of social dominance. Amer. Natur. 108: 818-830.

———. 1980. Behavioral mechanisms in ecology. Cambridge, Massachusetts, Harvard Univ. Press.

Mueller, H. C., D. D. Berger, & G. Allez. 1977. The periodic invasions of Goshawks. Auk 94: 652-663.

Newton, I. 1979. Population ecology of raptors. Vermillion, South Dakota, Buteo Books.

Pennycuick, C. 1972. Animal flight. London, Edward Arnold.

Peters, W. D., & T. C. Grubb, Jr. 1982. An experimental analysis of sex-specific foraging in the Downy Woodpecker, *Picoides pubescens*. Ecology 64: 1437-1443.

Poole, E. L. 1938. Weights and wing areas of 143 species of North American birds. Auk 55: 511-517.

Puttick, G. M. 1981. Sex-related differences in foraging behavior of Curlew Sandpipers. Ornis Scandinavica 12: 13-17.

Schipper, W. J. A., L. S. Buurma, & P. Bossenbroek. 1975. Comparative study of hunting behaviour of wintering Hen Harriers *Circus cyaneus* and Marsh Harriers *Circus aeruginosus*. Ardea 63: 1-29.

Siegel, S. 1956. Nonparametric statistics. New York, McGraw-Hill.

Snedecor, G. W., & W. G. Cochran. 1967. Statistical methods, 6th ed. Ames, Iowa State Univ. Press.

Snyder, N. F. R., & H. A. Snyder. 1970. Feeding territories in the Everglade Kite. Condor 72: 492-493.

———, & J. W. Wiley. 1976. Sexual size dimorphism of hawks and owls of North America. Ornithol. Monogr. No. 20.

Stiles, F. G. 1973. Food supply and the annual cycle of the Anna Hummingbird. Univ. California Publ. Zool. 97: 1-109.

———, & L. L. Wolf. 1979. Ecology and evolution of lek mating behavior in the Long-tailed Hermit Hummingbird. Ornithol. Monogr. No. 27.

Stinson, C. H., D. L. Crawford, & J. Lauthner. 1981. Sex differences in winter habitat of American Kestrels in Georgia. J. Field Ornithol. 52: 29-35.

Temeles, E. J. 1985. Sexual size dimorphism of bird-eating hawks: the effect of prey vulnerability. Amer. Natur. 125: 485-499.

Wolf, L. L., F. G. Stiles, & F. R. Hainsworth. 1976. Ecological organization of a tropical, highland hummingbird community. J. Anim. Ecol. 45: 349-379.

---

cess in White-crowned Sparrows. Condor 73: 77-80.

SHIELDS, W. M. 1982. Philopatry, inbreeding, and the evolution of sex. Albany, State Univ. New York Press.

SOUTHERN, H. N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). J. Zool. London 162: 197-285.

WILSON, E. O. 1975. Sociobiology, the new synthesis. Cambridge, Massachusetts, Harvard Univ. Press.

WRIGHT, S. 1940. Breeding structure of populations in relation to speciation. Amer. Natur. 74: 232-248.

———. 1943. Isolation by distance. Genetics 28: 114-138.

———. 1946. Isolation by distance under diverse systems of mating. Genetics 31: 39-59.

———. 1951. The genetical structure of populations. Ann. Eugenics 15: 323-354.

Repository for Voucher Photographs at VIREO

Photographs to document critical aspects of research methods and results in papers published in *The Auk* can be deposited with Visual Resources for Ornithology (VIREO) for long-term archival care. VIREO accession numbers for these photographs can then be published to enable subsequent access to the photographs for comparison, research, and teaching.

Voucher photographs should document critical and unique features of the published work, and normally should *not* be photographs published with the paper. Photographs of habitat and study-site slides are of exceptional importance for ecological and behavioral studies. Specific plumages, soft-body part colors, or morphological characters central to methods and results also would be appropriate, as would photographs illustrating novel techniques.

Preferably, authors will deposit original photographs with VIREO; if needed, a reproduction-quality duplicate is then returned. If the photographer must retain the original, then VIREO will place a reproduction-quality duplicate in archival storage. In this case VIREO requires temporary access to the original for duplication.

Authors interested in using this service should contact VIREO immediately after being notified of the acceptance of their papers for publication in *The Auk*: **VIREO, Academy of Natural Sciences, 19th and the Parkway, Philadelphia, Pennsylvania 19103 USA** (215-299-1069).