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The sixth annual meeting of the **Colonial Waterbird Group** will be held 4–7 November 1982 in Washington, D.C. A symposium on the feeding biology of waterbirds is planned. Papers given at the meeting are eligible, after refereeing, for publication in *Colonial Waterbirds*. Anyone wishing to contribute to either the symposium (deadline **1 September**) or general session (deadline **15 September**) should contact **Dr. Michael Erwin, U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland 20708.** Information concerning registration can also be obtained from Dr. Erwin.

THE ROLE OF MIGRATION AND WINTER MORTALITY IN THE LIFE HISTORY OF A TEMPERATE-ZONE MIGRANT, THE DARK-EYED JUNCO, AS DETERMINED FROM DEMOGRAPHIC ANALYSES OF WINTER POPULATIONS

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ABSTRACT.—This study of migratory Dark-eyed Juncos (*Junco h. hyemalis*) investigates differences in winter population structure and dynamics associated with north-south variation in wintering site and considers the relationships between these winter differences and population dynamics at other seasons. Banded juncos were captured and recaptured in several winters at four latitudes (42°–33.5°), and results were integrated with long-term United States Fish and Wildlife Service records of recoveries throughout the winter range.

The data suggest: (1) Populations wintering in the north experience higher winter mortality than populations wintering in the south. (2) Sex and age do not affect the probability of overwinter survival; therefore, dominance may not affect that probability. (3) Some individuals do and others do not return to the same wintering site year after year. Individuals that do not return tend to be those that have spent the first winter of life in the north, and these shift southward. (4) Annual mortality of northern and southern winter populations probably is the same. This conclusion is based in part on a comparison of north-south annual return rates and on logic arising out of the geographical distribution of the sexes during winter. In juncos, because males tend to winter north of females, greater annual mortality of northern winter populations would be expected to skew the primary and secondary sex ratios in favor of males. No evidence of such skews has been detected. (5) If annual mortality is the same, it is likely that southern populations suffer heavier mortality during their longer migrations and that these migration losses offset the advantage described in (1), above.

In north temperate-zone breeding species that migrate southward into an extensive winter range, distance traveled probably is correlated closely and positively with both mortality rate during migration and survival rate during winter. If these rates offset each other, annual survivorship among winter migratory populations (and among sedentary and migratory populations of partially migrant species) can be equal. Therefore, it is unnecessary to postulate for different winter populations either unequal reproductive success (von Haartman's hypothesis) or unequal year-to-year survival rates that balance out over the long term (Lack's hypothesis).

Migration can cause breeding populations to be redistributed in various ways in winter; e.g. they may mix randomly, or northern breeders may leapfrog southern breeders. Each variation in migration pattern would produce winter populations with predictable characteristics. We consider the extent to which winter junco populations have these characteristics. *Received 26 January 1981, accepted 30 September 1981.*

THE Dark-eyed Junco (*Junco h. hyemalis*), an abundant ground-feeding emberizid, migrates between a breeding range lying largely in the boreal forests of Canada and, in eastern North America, a winter range reaching from southern Ontario and the northern boundary of the United States almost to the Gulf of Mexico (Bent 1968). Because the winter range is so extensive, northern-wintering juncos spend that critical season (Lack 1954, Fretwell 1972) in cold and often snow-covered regions, whereas others, by migrating farther, move into progressively more moderate and even mild climates. Male juncos tend to winter north of females (Ketterson and Nolan 1976, 1979). Assuming an equal sex ratio on the breeding grounds—and both field study and theoretical considerations of sex ratio and mating systems support this assumption (see below)—the winter sexual separation necessarily implies that members of southern-wintering populations have migrated a greater average distance than members of

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northern populations. Further, in both sexes individuals produced in the preceding breeding season and adults exhibit differences, on the average, in winter distribution. The pattern of age distribution is stable from year to year and is complex (Ketterson and Nolan in prep.), but its most interesting feature is that the young of each sex tend to concentrate north of their adult counterparts. As with the sexual separation, this pattern implies differential migratory behavior associated with age, with adults traveling farther. When age classes of bird species separate in the winter range, it is usual for adults to make the shorter migration (Gauthreaux 1978), although the pattern we find in the junco has been observed in the American Goldfinch (*Carduelis tristis*) (A. Middleton pers. comm.) and the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) (King et al. 1965).

Predicting that juncos that winter in the north would experience greater overwinter mortality than those that migrate into the south, we also expected that annual survivorship of southern winter populations would be higher. A corollary of this latter prediction is that members of such southern populations should have lower reproductive success, assuming that fitness of juncos does not vary according to the latitude of the wintering site. As we here report, the expectation about unequal overwinter mortality appears to be correct, but the evidence does not support the prediction that wintering in the south confers greater annual survivorship. This implies that southern winterers have higher mortality than northern winterers at some other stage of the annual cycle, and the most probable occasion for such compensatory mortality is during their longer migrations.

Recent evolutionary speculations have stressed how little is known of the impact of migration on survival and reproduction and have urged that more attention be devoted to acquiring data that will further understanding of these subjects (Baker 1978, Gauthreaux 1979, Krebs 1979, Dingle 1980). For such inquiries the Dark-eyed Junco provides an exceptionally good system. Its extensive winter distribution and sex-age differences in distance migrated permit comparison of seasonal and annual survivorship among conspecific populations that differ greatly in the way they balance the risks of migration against the rigors of winter.

In this paper we present data on minimum overwinter survivorship and minimum annual survivorship in northern- and southern-wintering populations that we sampled by capture-recapture techniques at the beginning and end of single winters and also in successive early winters. Interpretation of such data requires that death and dispersal be separated out as factors affecting the recapture data. We therefore analyze United States Fish and Wildlife Service (USFWS) Bird Banding Laboratory records bearing on the question of north-south variation in the winter dispersal tendency of juncos in the eastern United States. We also examine these USFWS records for time elapsed between banding and recovery, which we take as an estimate of survivorship, and compare them with a long-term estimate of survival of an Indiana sample.

Our results, like the USFWS data that we consider, are limited to eastern winter populations. The breeding sites of these birds were unknown, and all references to northern and southern juncos are to winter populations, except where it is explicitly stated otherwise.

METHODS

Capture-recapture data.—Juncos end their autumnal migration about 1 December and begin spring migration about 1 March (evidence for this is reviewed in Ketterson and Nolan 1976), with indications that few move very far in the interim (see below). Therefore, individuals found from December through February we consider to be winter residents. We captured juncos at a series of sites in early winter (December, except that an occasional effort extended into the first few days of January), then made recapture efforts in late winter (February, except that one effort extended into early March) and/or in the subsequent December; all unmarked juncos, whenever caught, were given USFWS bands. Early-winter sampling was at Kalamazoo, Michigan (42°N); Bloomington, Indiana (39°N); Clemson, South Carolina (34.5°N); and Birmingham, Alabama (33.5°N) in the winters of 1976–1977, 1977–1978, 1978–1979, and, except for Alabama, 1979–1980 (Fig. 1). Late-winter sampling was restricted to the Indiana and South Carolina sites in 1977–1978 and 1978—1979.

Long-term mean temperatures for the period December–February and annual snowfall at the four capture-recapture sites follow: Michigan, −4.0°C, 139.9 cm; Indiana, −0.6°C, 59.9 cm; South Carolina, 6.5°C, 8.4 cm; Alabama, 7.8°C, 4.6 cm (U.S. Weather Bureau 1932).

Each capture effort was limited to a 3- to 6-day

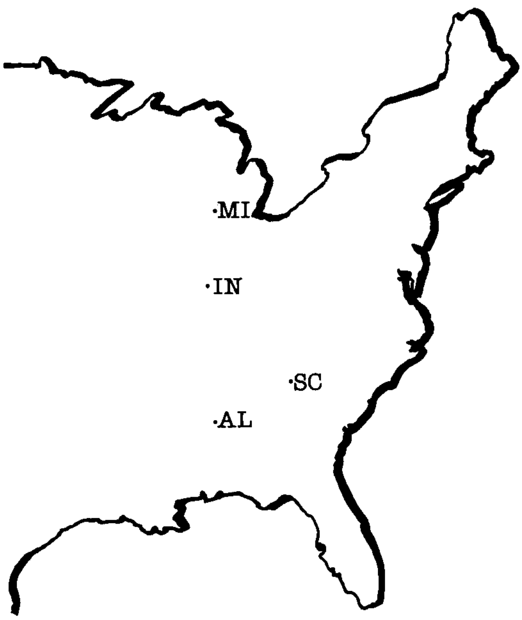

Fig. 1. Sites at which juncos were captured.

period of intensive field work that had been preceded by several days of baiting at the spots (hereafter called subsites) at which nets and traps were set up. One to four subsites were sampled at each site. At the end of all capture efforts, baiting stopped, except in Michigan, at one subsite in South Carolina, and at one subsite in Alabama. We made every attempt to standardize capture methods from site to site, with the exception that weather differences affected the ease of capture and therefore caused the length of capture efforts to vary. For example, snow usually covered the ground in Michigan and did so in late winter in Indiana and once even in South Carolina; this led juncos to concentrate at our bait and let us abbreviate our operations. At all sites on the last day of an effort, the proportion of recaptured individuals that had been caught and banded during that effort was approximately the same.

We sexed juncos by examination of plumage traits and wing length (Ketterson and Nolan 1976), performing laparotomies when in doubt. The degree of skull ossification in early winter revealed which individuals had hatched in the preceding breeding season (herein called young) or in some earlier breeding season (herein adult). In late winter, juncos caught for the first time were aged on the basis of plumage, wing length, and eye color (Ketterson 1979b). This method has proved 93% accurate in cases in which we tested late-winter age determinations of previously banded individuals against our original age determinations based on skull examination. Only birds released in good condition were considered in calculating recapture rates. A few were marked in one effort, not caught in the next, then recaptured in still the next. These we treated as having been present during the intervening effort, even though we had not caught them, but, having counted them as present on that one occasion, we eliminated them from subsequent recapture calculations.

Samples collected under the time constraints described are smaller than ideal for statistical purposes, and for some comparisons we have been compelled to pool across years. We have also combined the data from Michigan and Indiana, which we regard as northern wintering locations, and from South Carolina and Alabama, which we regard as southern. We tested for statistical homogeneity before such combining; despite nonhomogeneity in one case, we combined, because to do so produced a conservative result that did not affect the argument.

Other Indiana data.—We draw also on the results of two independent studies carried out near Bloomington at locations other than those referred to above and involving other juncos. (1) In December 1978 and 1979, as the first part of an investigation (in prep.) of dispersal within single winters, we caught, banded, and released juncos at eight stations, each 1.5–2 km apart, along a transect. In February 1979 and 1980, we again trapped and netted at these stations. Sexing and aging were as described above. We present these data here in order to show the sex-age structure of the Bloomington population at the beginning and end of two winters and to draw conclusions about the relative overwinter mortality of the different sex-age classes there. It is important to note that the structure at all eight stations was about the same; we detected no sex or age segregation in early or late winter. Recapture rates are not shown, although they were very much like the Indiana rates presented in Table 1, because our methods were different from those described above. (2) For a more accurate measure of the annual survivorship of juncos that winter in Indiana, we selected 128 site-faithful individuals caught between 1961 and 1977 at two sites at which trapping and netting were carried out nearly daily from October into May (the approximate limits of the junco's occurrence in Indiana). Male and female numbers in this sample were representative of the proportions in the Bloomington winter population; the sexes did not differ significantly in returns and accordingly were pooled. All 128 were present in at least two winters and three were present in six; not every bird was caught in an uninterrupted series of winters. Ignoring calendar years, we formed a composite in which each individual's banding year was the base line and subsequent years were +1, +2, etc. As is typical in avian survivorship studies (Nolan 1978: 466 and citations therein), the proportion of any year's birds that were present the following year did not change as the birds aged. We applied Caughley's (1977: 151) method to estimate

TABLE 1. Rate of recapture in late winter of juncos marked in early winter according to sex, age, year, and location.[a,b,c]

	Male		Female		Classes combined
	Adult	Young	Adult	Young	
Indiana					
1977–1978	6/27	2/36	0/4	0/10	8/80
1978–1979	4/41	6/42	1/9	3/19	16/118
Years combined	15% (68)	10% (78)	8% (13)	10% (29)	12% (198)
South Carolina					
1977–1978	8/31	6/15	11/22	5/13	30/81
1978–1979	7/15	3/7	12/21	8/12	30/55
Years combined	33% (46)	41% (22)	53% (43)	52% (25)	44% (136)

[a] Sample sizes are in parentheses and represent the number of juncos marked in early winter and released in good physical condition at a location that was sampled in late winter. The size of the combined sample is sometimes greater than the sum of samples of the respective sex-age classes, because a few individuals marked were of unknown sex or age.

[b] Late-winter recapture rates of the sex-age classes at a location were compared after combining data for the two different years. In Indiana, the sex-age classes were equally likely to be recaptured [$\chi^2 = 0.94$, df = 2, n.s. (female age classes combined because samples small)]. The same was true of South Carolina ($\chi^2 = 4.72$, df = 3, n.s.).

[c] Late-winter recapture rates of a sex-age class at the different locations were compared after combining data for the 2 yr. Each sex-age class was significantly more likely to be recaptured in South Carolina than in Indiana (adult males: adj. $\chi^2 = 4.15$, df = 1, $P < 0.05$; young males: adj. $\chi^2 = 9.36$, df = 1, $P < 0.01$; adult females: adj. $\chi^2 = 6.77$, df = 1, $P < 0.01$; young females: adj. $\chi^2 = 9.26$, df = 1, $P < 0.01$).

the annual mortality rate of the group. Use of site-faithful birds was necessary, of course; we recognize the possibility that nonfaithful individuals may have a different mortality rate.

USFWS data.—The Bird Banding Laboratory stores information on the date and location of initial banding and recovery as well as on the method of recovery, but it records locations only according to their 10-min blocks of latitude and longitude (roughly speaking 100 km^2 in the eastern United States). Recoveries made by bird banders are identified as such. The fact that banders are concentrated in more populous areas, especially in the northeastern United States, would bias the estimates made herein if recoveries by banders were included in our analysis, and we therefore considered only juncos recovered dead by the general public (i.e. we omitted cases with the Laboratory's recovery code numbers 10, 16, 29, 51–53, 87, 89, 99). From the resulting records for the years 1921 through August 1976, we selected the 368 cases of individuals that were both banded and recovered in winter (December–February) east of 106°W longitude. Each case we categorized according to (1) latitude of initial capture location, (2) whether recovery was during the winter of banding or during a subsequent winter, and (3) whether recovery was at or away from the initial capture location. We then examined the results for latitudinal trends in tendency to disperse from the banding location, either in the winter of initial capture or a later winter. When banding and recovery were in different winters and at different locations, we noted the directional relationship between the locations. If the locations were the same, we noted the interval in years between the two events.

Because juncos cannot be sexed reliably without considerable experience and the method of aging by skull ossification is both relatively recent and not used by all banders, we could not analyze USFWS data for possible variation associated with sex and age. We recognize that the USFWS data set is small, with few cases from the south. Further, the areas encompassed by 10-min blocks of latitude and longitude are much larger than the areas of our capture sites. This presents a difficulty, described in detail below, in combining USFWS recovery data with our recapture data. Of course, the size of the 10-min blocks has no effect on the validity of comparisons of northern and southern juncos when these comparisons are restricted to the USFWS data.

RESULTS

Recapture in winter of banding.—Minimum overwinter survivorship, as estimated by the percentage of juncos that were recaptured at the end of winter, differed geographically. A much larger proportion of South Carolina birds than of Indiana birds (44% vs. 12%) was recaptured in late winter (Table 1). A February snow storm, an unusual event in South Carolina, may have been partly responsible for the high recapture rate there. Even in the winter in which February weather in South Carolina was normal (1977–1978), however, the recap-

TABLE 2. Sex-age[a] structure (percentages of individuals) of early- and late-winter samples of juncos in Indiana and South Carolina.

		Male		Female	
	n	Adult	Young	Adult	Young
Indiana[a,b]					
December 1978	395	28	42	10	21
February 1979	400	24	45	9	22
December 1979	346	17	52	10	21
February 1980	320	22	44	13	22
South Carolina[a,c]					
December 1977	87	37	17	28	18
February 1978	170	23	15	34	28
December 1978	132	26	17	33	24
February 1979	104	34	10	41	15

[a] Indiana samples were caught in a study of dispersal at eight sites; individuals in them differ from those in all other tables. South Carolina juncos were caught in the overwinter survival study. See text.

[b] Indiana seasonal comparisons of sex-age ratios, December vs. February 1978–1979: $\chi^2 = 1.90$, df = 3, n.s.; December–February 1979–1980: $\chi^2 = 5.10$, df = 3, n.s.

[c] South Carolina comparisons of sex-age ratios, December vs. February 1977–1978: $\chi^2 = 7.96$, df = 3, $P < 0.05$; December vs. February 1978–1979, $\chi^2 = 5.95$, df = 3, n.s.

ture rate was significantly higher than the Indiana rate, and all Indiana late-winter recapture efforts were conducted after heavier snow storms than the one in South Carolina.

Comparing sex-age classes within each site, the late-winter recapture rates in Indiana were statistically indistinguishable for all sex-age classes, and the same was true in South Carolina (Table 1). In accordance with this evidence that at neither latitude did age or sex affect the probability of overwinter survival, data from our study of winter dispersal in Indiana (Table 2) reveal no statistical change in sex-age ratios between early and late winter and certainly suggest no disadvantage associated with being immature or female. When the structure of December and February samples caught in South Carolina is compared (Table 2), we see that in one winter it remained the same and in one it changed. In the latter, adult males were less frequent in late February–early March, and all females were more frequent. If this was not sampling error, it might mean that old males had begun to migrate (in which case our already high overwinter recapture rate might not be high enough); but it is most unlikely that it means old males survive winter in South Carolina less well than do females.

TABLE 3. Percentages of juncos recorded by United States Fish and Wildlife Service (1921–1975) as recovered in winter at the place of original capture, according to latitude of place of capture: an estimate of the relationship between dispersal and latitude.[a,b]

	Recovered in subsequent winter		Recovered in same winter	
Latitude of place of capture	Total cases	Percentage at place of capture	Total cases	Percentage at place of capture
45–44	2	100	3	100
43–42	25	52	73	95
41–40	45	53	75	91
39–38	42	74	60	90
37–36	6	83	6	83
35–34	8	88	9	77
33–32	3	100	11	100
	131		237	

[a] Data were taken from files of the Banding Laboratory of the United States Fish and Wildlife Service and restricted to juncos banded in the months December–February and recovered in those months in the same or in any later winter. Banding and recovery sites were located between longitude 70°W and 105°W. The Laboratory records locations only as within 10-min blocks of latitude and longitude; thus, recovery at the place of capture means within the same block. To avoid possible bias associated with the northward concentration of bird banding stations in the United States, the sample is confined to juncos recovered other than by a bird bander. Note that most initial captures were in the northeastern United States (Fig. 2).

[b] In correlating the percentage of recovery at the place of original capture (i.e. fidelity to a 10-min block as defined in footnote a) and latitude of place of original capture, intervals of latitude represented by fewer than five recoveries are ignored. For recoveries in a winter subsequent to that of original capture, r_s (Spearman's rank) between latitude and fidelity = 1.0, $n = 5$, $P < 0.05$. For recoveries in same winter as that of original capture, $r_s = 0.14$, $n = 6$, n.s.

USFWS data: recovery in winter of banding.—When analysis is limited to USFWS recoveries during the winter of initial banding, no geographic variation in overwinter dispersal is evident. Only 18 juncos among 237 that were thus recovered had moved to a different 10-min block, and such dispersal was as frequent among southern as among northern birds (Table 3). We interpret this below as support for the view that the difference in overwinter recapture rates in Indiana and South Carolina reflects, at least in part, differential winter mortality. However, if juncos that disperse from northern banding sites tend to move very short distances whereas those from southern sites move long distances, the USFWS method of recording only 10-min blocks would underestimate the relative numbers of northern dispersers and make the

TABLE 4. Rate of return from one December to the next according to sex, age, and location.[a,b,c]

	Males		Females		Classes pooled
	Adult	Young	Adult	Young	
North					
Michigan	19/141	4/165	1/43	2/64	26/413
Indiana	6/79	5/95	0/16	1/36	12/226
Combined	11%	3%	2%	3%	6%
	(220)	(260)	(59)	(100)	(639)
South					
South Carolina	5/62	7/40	4/78	5/44	21/224
Alabama	1/9	1/6	4/22	3/14	9/51
Combined	8%	17%	8%	14%	11%
	(71)	(46)	(100)	(58)	(275)

[a] The numbers of birds recaptured from among those released in good condition at the capture site in the preceding winter are presented for each location. A few juncos were recaptured only after an intervening winter, and these were considered to have been present in the first postbanding winter. Juncos were marked in four winters, and recapture efforts were made in three at Michigan, Indiana, and South Carolina. Only two recapture efforts were made at Alabama. The percentages were computed on the combined northern and combined southern locations.

[b] Comparisons of return of each sex-age class to northern (Michigan, Indiana) and southern (South Carolina, Alabama) locations follow: adult males, north vs. south, adj. $\chi^2 = 0.23$, df = 1, n.s.; young males, north vs. south, adj. $\chi^2 = 11.28$, df = 1, $P < 0.001$; young females, north vs. south, adj. $\chi^2 = 4.85$, df = 1, $P < 0.05$. For all classes pooled, rate of return to the south was significantly higher (adj. $\chi^2 = 7.07$, df = 1, $P < 0.01$).

[c] Frequency of return of the sex-age classes differed at northern sites ($\chi^2 = 17.87$, df = 3, $P < 0.001$) but not at southern sites ($\chi^2 = 3.80$, df = 3, n.s.).

data useless for our purposes. At the present time, we can say only that we have no reason to expect such a geographical difference.

Recapture subsequent to winter of banding.—The percentage of birds recaptured in a winter subsequent to that of banding, i.e. the return-recapture or minimum annual survival rate, showed both geographical variation and variation according to sex-age class. When data pooled from Michigan and Indiana without respect to sex or age and combined across all years are compared to similarly pooled and combined data from South Carolina and Alabama, return-recapture at the northern sites (6%) was significantly lower than at the southern sites (11%) (Table 4).

When the data are broken down by sex and age, the frequency of returns at the combined northern sites differed for the four classes ($P < 0.001$), but this was attributable to variation between the two most numerous classes: adult males returned and were caught more frequently than young males (11% vs. 3%, $P < 0.001$) (Table 4). This difference, in conjunction with the preponderance of males in the north, also causes the northern adult rate to exceed the rate for northern young (9% vs. 3%) significantly. Sample sizes do not permit statistical comparison of northern female age classes (2% vs. 3%), because so few adult females winter in the north. Similarly, adult females cannot be compared statistically with adult males, although the percentage of adult male returns was higher (11% vs. 2%).

In contrast to the variation between northern age classes and also between northern sex classes, all sex-age classes in the south were recaptured with statistically equal frequency.

Turning to sex-age comparisons between north and south, young northern juncos of each sex returned and were recaptured at the banding site less often than young southern juncos of the same sex (males: 3% vs. 17%, females: 3% vs. 14%). Adult male returns were the same, north and south; again the small northern sample of adult females prevents statistical comparison (males: 11% vs. 8%, females: 2% vs. 8%).

Because we believe the low return rate of northern adult females to be largely a product of sampling error—recall that the Indiana sample of site-faithful individuals showed no sexual bias—we summarize and interpret Table 4 as follows. The difference in the pooled return-recapture rates between northern and southern locations is apparently largely or entirely due

Fig. 2. Initial capture location and recovery location of juncos shown by USFWS records to have been captured and recovered in different winters and at different places. For clarity, movements of less than 30 min are not plotted. See text for other details. Each line represents an individual junco. The dot is at the original capture location and the arrow point is at the recovery location.

either to lower survivorship or lesser site fidelity among young northern juncos of both sexes. These alternative possibilities are discussed below.

USFWS data: recovery subsequent to winter of banding.—We consider the extent to which the juncos in the USFWS sample tended to select a new location in the later winter. Of 131 individuals banded in one winter and recovered in another, 46 had moved away from the 10-min block in which they had first been caught (Table 3). This considerable shift was largely confined to birds first captured at higher latitudes (Table 3). The concentration of data from more northerly locations makes statistical comparison somewhat arbitrary. Table 3 employs a Spearman's rank coefficient, but here we compare the subsets from latitudes 42–45° (15 returns in 27 cases), 40–41° (24 returns in 45 cases), 38–39° (31 returns in 42 cases), and 32–37° (15 returns in 17 cases): $\chi^2 = 9.16$, df = 3, $P \leq 0.05$. Both approaches indicate that site fidelity was greater to more southerly locations. In addition, a directional component is apparent in cases in which individuals chose new sites. Most tended to move southward, sometimes great distances, in later years (Fig. 2); among 28 cases of latitudinal shifts equal to or greater than 30 min, i.e. shorter movements and east-west movements excluded, 24 were southward.

This interesting result caused us to reanalyze the initial capture (banding) dates of the juncos that shifted to new sites. Our question was whether these individuals really had been winter residents where first caught: if the capture dates had fallen in early December, this might support the view that these birds were still migrating southward when caught, i.e. had not necessarily resided in different places in the two winters. No such support was found, however. Only two banding dates were prior to 18 December (on 11 December of different years), and seven and nine, respectively, were in January and February.

USFWS data: life expectancy.—We examined the number of whole years elapsed between banding and recovery of the 85 USFWS juncos that were taken in two different winters in the same 10-min block and that had therefore been exposed to the same climates, if not weather, in both those winters (and probably in any intervening winters as well). Treating years elapsed as an estimate of life expectancy at the time of banding, we looked for variation according to latitude. No variation is detectable (Table 5). Approximately half the juncos that survived to be recovered in a winter subsequent to that of banding had lived at least 2 yr after first capture, regardless of the latitude of the banding site.

Translating the data in Table 5 into a survival rate and making the usual assumption of constant annual mortality with advancing age, the survival rate is 54%.

Survival of site-faithful Indiana juncos.—Caughley's method estimates the annual survival rate of the juncos site-faithful to Bloomington to be 53%, as follows:

$$\bar{q} = 1 - \frac{m_1 + m_2 + m_3 + m_4 + m_5}{m_0 + m_1 + m_2 + m_3 + m_4}$$

$$\bar{q} = 1 - \frac{99}{187}$$

$$\bar{q} = 0.47$$

where $\bar{q}$ = finite rate of annual mortality and m_n = number of marked juncos caught at time n.

DISCUSSION

OVERWINTER SURVIVORSHIP AND DOMINANCE STATUS

Indiana samples, which were large as well as diverse in method and location of collection (Tables 1 and 2), were alike in indicating that sex and age did not influence the probability that an individual would survive the winter. As discussed above, we interpret the less numerous data from South Carolina as indicating that the same was true there (Tables 1 and 2).

TABLE 5. Years elapsed between banding and recovery of juncos recovered in some subsequent winter at the banding location, according to latitude: an estimate of the relationship between wintering latitude and life expectancy (USFWS data).

Latitude[a]	Total cases[a]	Recovered more than 1 yr (winter) after banding[b]	
		n	Percentage
45°–42°	15	8	53
41°–39°	44	26	59
38°–36°	16	7	44
35°–32°	10	5	50
	85	46	

[a] Sample consists of juncos recovered in same 10-min block at least 1 yr (one winter) after winter of banding. Extreme northern and extreme southern bands of latitude are 4° wide; middle intervals are 3° wide in order to make sample sizes comparable.

[b] Comparing latitudes for number of juncos recovered more than 1 yr (winter) after banding and number recovered only 1 yr after banding, $\chi^2 = 1.20$, df = 3, $P > 0.5$; time elapsed (survived) between banding and recovery is independent of latitude.

These results have interesting implications for theories about the importance of dominance, which until quite recently (Ketterson 1979b, Baker et al. 1981, Rohwer and Ewald 1981) has been generally accepted as affecting survival.

The sex-age classes of juncos differ in dominance rank when winter flocks assemble at food (Balph 1977; Ketterson 1979a, b), and in juncos dominance rank has been related to survival in nature (Fretwell 1969) and in the laboratory (Baker and Fox 1978). These facts would lead to the prediction that overwinter survivorship varies according to the rank associated with each sex-age class, that is, in descending order from adult males to young males, adult females, and young females. Survivorship differences of this kind might have been expected to be especially conspicuous in the severe winters of Indiana. Our observations to the contrary suggest either (a) that dominance played no role in the evolution of geographic variation in winter sex-age ratios (see Myers 1981), because it does not influence overwinter survivorship, or (b) that dominance did play a role and has produced a pattern of varying ratios in which subordinate classes suffer differentially only when population structures or densities shift from those that obtained during this study. Aviary experiments in which sex-age ratios are varied, food restricted, and behavior and survivorship noted are underway in an effort to pursue this problem.

DIFFERENTIAL OVERWINTER MORTALITY IN NORTH AND SOUTH

The lower overwinter recapture rate in Indiana as compared to South Carolina, when considered with the USFWS data suggesting no geographic difference in overwinter dispersal, points to greater winter mortality among northern juncos. That juncos do die during severe weather is a fact. Their emaciated carcasses are found after periods of prolonged snow cover and low temperature (Roseberry 1962, Johnston 1962, Graber and Graber 1979, pers. obs.), which are frequent in the north and rare or absent in the south. Furthermore, our 2-yr study of dispersal in Indiana and over 20 yr of intensive winter banding there at several sites about 0.1–0.3 km apart have revealed little dispersal and none on a scale that could produce the substantial difference in Indiana and South Carolina overwinter recapture rates.

We conclude that very probably northern juncos of all sex-age classes die more frequently in the average winter than do southern juncos. Because our data were obtained during only two winters, we do not propose that they are necessarily representative of the long-term difference between Indiana and South Carolina.

FACTORS OFFSETTING DIFFERENTIAL OVERWINTER MORTALITY IN NORTH AND SOUTH

Theoretical considerations.—If the conclusion just reached is correct and if, as we take for granted, choice of winter site is governed by natural selection, the mortality difference associated with wintering in the north must be offset by advantages that tend to equalize the fitness of members of northern and southern winter populations. (We assume that fitness does not vary according to location of wintering site, i.e. that directional selection is not in the process of shifting the junco's winter distribution either southward or northward.) The compensatory advantage(s) of wintering in the north must take the form of (1) higher survivorship than that of southern juncos during some other season(s), thus bringing annual survivorship toward equality, or (2) greater reproductive success, or (3) a combination of these.

Investigation of the nature of the putative advantage accruing to northern winterers encounters, at the threshold, the fact that data on comparative reproductive success are nonexistent and probably unobtainable. Getting them would require that members of winter populations be traced to their summer locations in a vast breeding range. Good estimates of long-term annual survival rates of northern and southern winter populations can be developed, however, and comparison of these will give an idea whether, and to what extent, differential reproductive success is operating to equalize fitness. If long-term annual survivorship is found not to vary with the latitude of the wintering site, the assumption of stability in the existing winter distribution would exclude the possibility of unequal long-term reproductive success. There would remain only the alternative that seasonal survivorship is unequal, not simply in winter but during other segments of the year as well.

The data to be discussed below suggest to us that the average annual survival rates of northern and southern winter populations are the same. We argue that southern winterers probably suffer heavier mortality during, and because of, their longer migrations and that this equalizes their survivorship with that of northern winterers.

Evidence for equal annual mortality.—(1) The life expectancy of juncos banded in one winter and recovered in the same 10-min block in a later winter, as recorded by the USFWS, was invariant with latitude. The sample is not large, but it gains strength from having been compiled over many years. Probably the result is not much distorted by random annual variation.

(2) Our estimated annual survival rate of 53% among site-faithful Indiana juncos agrees very closely with the independent estimate, 54%, from the USFWS data. It is important to note that 53% is well within the range of annual survival rates reported for temperate-zone passerines (Farner 1955, Greenberg 1980, Searcy and Yasukawa 1981). If our estimate is representative of juncos that winter in Indiana, there is no a priori reason to expect South Carolina juncos to have higher survivorship, nor is it necessary to suppose that Indiana popu-

lations require some unusual reproductive advantage to maintain equal fitness with southern juncos.

(3) The return-recapture rates in Table 4 show equal minimum annual survival of adults in northern and southern winter populations. The 53% Indiana survival rate obtained by continuous efforts throughout the junco's residence there shows that in Indiana sampling lasting only a few days fails to recapture many banded individuals that are in fact present. That this is also true at our other sites is indicated by the fact that at all of them we sometimes caught banded juncos that had escaped capture in the preceding effort. We assume that the probability of failing to recapture an individual even though it was present was equal at all sites. If this conservative assumption is correct, annual survivorship of adults in those samples did not vary with latitude.

In contrast to the adult rates, the return-recapture rate of northern young fell below the rate for northern adults, for southern young, and for southern adults, all of which were statistically indistinguishable. Despite this difference, for two reasons we believe that northern young survived the year between sampling and resampling as well as did the other classes. (1) The survival of northern adults from December to December would not be expected to be higher than that of northern young if it were no higher in the first 3 months of that 12-month period. Any survival disadvantage associated with inferior age and experience should show up early, particularly because the early part of the year used in our calculations was winter. But Tables 1 and 2 reveal no disadvantage; northern young were as likely as adults to be recaptured in late winter, and in each of two winters rather large Indiana samples revealed no change in age ratios between December and February. Evidently, young juncos have passed beyond the "initial juvenile period of higher mortality" (Farner 1955: 403) by December. In this they are like many other north temperate-zone passerines, for which, as a rule of thumb, 1 January is often taken as the date at which life expectancy stabilizes at the adult rate (see discussion and citations in Farner 1955). (2) The low return-recapture rate of northern young can be explained plausibly by supposing that some survivors of that age class choose new sites in their second winter and thus are responsible for the lower fidelity to northern latitudes revealed in the USFWS data. We emphasize that the junco's age distribution in winter would have led us to predict a lower return-recapture rate of northern young even before that lower rate was found. That is, a distribution in which young tend to winter north of adults could be maintained year after year only by lower survivorship of young than of adults between December sampling operations (a possibility just considered and dismissed) or by choice of a different and more southerly second winter site by some individuals that have spent their first winter farther north. Notably, Spaans (1977) has reported similar between-winter shifts toward milder climate in the Starling (*Sturnus vulgaris*).

In sum, the return-recapture rates, the USFWS records, and our winter demographic data converge from independent directions and point to equal annual mortality of northern and southern wintering populations.

Consequences of unequal annual mortality.—Without regard to the affirmative evidence for equal annual mortality, unequal mortality of winter populations would have demographic consequences that can be predicted from, or tested against, theory. All the expected consequences would be observable in the field, and none has been observed.

Any hypothesis that northern winter populations have lower annual survivorship must also take account of, and be reconciled with, five points that we regard as facts or fair assumptions about the junco. (1) More males winter in the north, more females in the south. (2) Overwinter survival of the sexes in the north is equal. (3) Southern juncos are more likely to survive winter than are northern; therefore, because of points 1 and 2, fewer females than males die during winter. (4) Mortality of adults, i.e., experienced migrants, is probably no higher during autumn migration than during spring migration, because weather is less certain at the time of spring migration, and the preceding year's seed crop is depleted after having supported consumers throughout the winter. (5) The hazards of migration per unit of distance traveled are probably the same for females as for males; if the two sexes depart from the same spot for the same destination, females should be at least as likely as males to survive and arrive. This assumption seems reasonable in view of the absence of any sex role associated with the behavior involved in

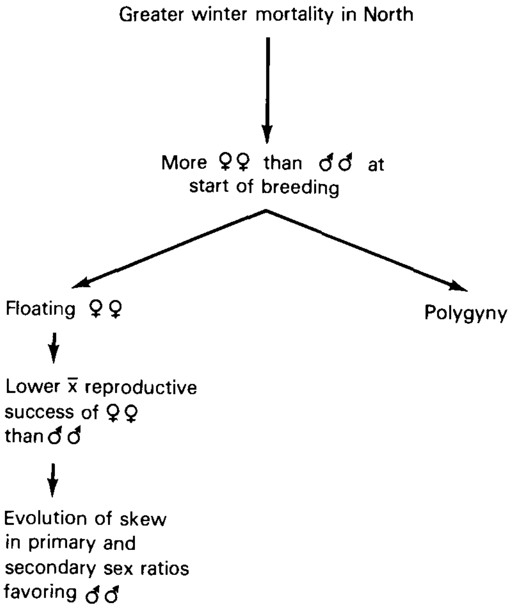

FIG. 3. Possible evolutionary consequences of a situation in which winter mortality, and as a result annual mortality, of males exceeds that of females, producing an excess of females among potential breeders. See text.

migrating. If a bias does exist, it is likely to be against males, because males migrate earlier (spring only, pers. obs.), when weather conditions are both less predictable and less moderate.

In addition to the five points just enumerated we make another assumption, which, though it is conservative, must be justified. In the next section we present our reasons for assuming (6) that survivorship of the sexes is approximately equal during the breeding season, but for the present we simply proceed on the assumption.

Now suppose a breeding population, its sex ratio at unity and its members about to migrate varying distances into the winter range. Under the hypothesis that annual mortality rates of winter populations are unequal because of higher survivorship of southern winterers, more females than males from this breeding population will be alive at the start of and during the next breeding season. The imaginable consequences of a breeding-season surplus of females are either (1) that some females will not get mates or (2) that some females will mate polygynously (Fig. 3). The first of these possibilities results in greater reproductive success for males, the minority sex, than for females (*sensu* Fisher 1930). Such a situation, in which a floating population of females exists, will not be stable: instead, the sex ratio at conception (hereafter, primary sex ratio) would be expected to evolve toward a skew in favor of males and this skew would persist in the sex ratio at the end of parental care (hereafter, secondary sex ratio). The second alternative, polygyny, supposes that this mating system would evolve as a response to an unbalanced tertiary (breeding) sex ratio. Such an evolutionary sequence was at one time accepted as a satisfactory mechanism to account for avian polygyny, but it is now generally rejected, because it probably confuses cause and effect (Selander 1965, Orians 1969, Emlen and Oring 1977; but see Wiley 1974).

Field data bearing on the alternative possibilities just presented are as follows. *Mating system:* Juncos are reported to be, like the great majority of birds (Lack 1968a, Verner and Willson 1969), monogamous. During 8 weeks (spread over 4 yr) of intensive study of juncos in July and early August, when most females have dependent young, we have found 30–35 broods, all of them closely attended by an adult male and an adult female. Sexual dimorphism of juncos is slight, which supports the view that monogamy is their normal mating system (Emlen and Oring 1977).

Secondary sex ratio: At Wawa, Ontario, we netted randomly for 3 days in early September 1979 and for 10 days at the end of July 1980 and caught 43 newly independent young that were still in complete juvenal plumage. Of these, 22 were male and 21 female. (The birds were held in captivity and sex determined in the usual way after postjuvenal molt was completed.)

Breeding sex ratio: We have seen no evidence of a floating nonbreeding female population. Instead, all females that we have netted randomly, even early in the breeding season (June), have had incubation patches. Twice we have observed males, known to be unmated, advertise for at least 2 weeks in June.

In sum, the hypothesis that southern-wintering juncos have greater annual survivorship implies a sexual difference in mortality because of the clinal variation of the winter sex ratio. None of the consequences of a sexual difference in annual mortality has been observed, and what field evidence there is tends to falsify the hypothesis.

Mortality at other seasons.—If further evidence should establish that annual mortality is invariant for northern and southern populations sampled in December, during what season(s) is it likely that southern winterers compensate by experiencing higher mortality than northern?

We turn first to the breeding season. It is most unlikely that higher mortality during breeding would be *caused* by wintering in the south, but there are two possible reasons for a *correlation.* (1) If breeding location determined winter location in the sense that members of breeding populations wintered together, e.g. if northern breeders were northern winterers, latitudinal variation in some factor causing summer mortality might offset latitudinal variation in winter mortality. Although we can conceive of clinally varying summer mortality (e.g. as the result of distribution of predators), we reject this first alternative, because breeding populations do not remain intact in winter: the partial sexual separation and, probably, the partial age separation at that season eliminate this possibility. (2) Higher survivorship by southern winterers would tend to be offset by higher summer mortality if breeding females had a greater mortality rate than breeding males. We know of no evidence bearing on a sexual difference in breeding mortality, except that we have not seen dependent young being tended by only one parent (see above). If, however, excessive male mortality in winter were balanced by excessive female mortality in summer, a nonbreeding surplus of females would arrive—and for a time survive—on the breeding range, unless the primary and secondary sex ratios shifted to adjust for the greater reproductive success of males or unless some mating bonds were polygynous. These points have been examined above, where it was concluded that existing evidence does not point to a surplus of females, or a skewed secondary ratio, or a polygynous mating system. We therefore propose that southern winter populations compensate for their greater overwinter survivorship by greater mortality during, and because of the increased risks involved in, their longer migrations.

If annual mortality of southern winterers is equalized during their migrations, in an average year approximately the same number of males and females will arrive on and leave the breeding grounds. Males will predominate in the winter range at the beginning of winter, be in the minority just before spring migration begins, and be in parity again after migration mortality has reduced southern winterers, with their disproportionate female numbers.

It may be objected that a substantial increase in mortality during migration into the south is unlikely when the difference in distance traveled to southern sites is probably at most about 1,000 km, approximately the distance separating our Michigan and Alabama sites. It is true that some juncos have been found (Johnston 1962, Helms et al. 1967) to carry migratory fat reserves sufficient to permit them to cover 1,000 km in only two flights, with a stopover to fatten up, although we see few fat juncos in spring and autumn in Indiana. Theoretical arguments and limited evidence (reviewed by Baker 1978: 679) suggest, however, that overland migrants do not make long flights, whatever their fat reserves. Instead, they are believed to migrate in numerous short moves separated by stopovers, a conclusion that Johnston (1962) drew for juncos after field and experimental physiological study of North Carolina populations. At each stop the migrant may confront dangers arising out of unfamiliarity with locations of food, shelter, and refuge from predators. We imagine such dangers to be considerable and to increase in stepwise fashion with the number of stops. So far as we know, the extent to which hyperphagia leads birds to run greater risks of predation has not been investigated, but the increase may be important. Certainly, hungry, free-living juncos will tolerate the close approach of humans before interrupting their foraging (e.g. when snow covers the ground), and we have seen many apparent migrants with such low energy reserves that they can be assumed to have been hungry. For example, juncos caught in midafternoon in Indiana during the migration seasons sometimes starve before morning if held at room temperature without food. In contrast, Indiana juncos caught in winter normally can fast for 40–45 h at 4°C and still recover (Ketterson and Nolan 1976, 1978; Stuebe and Ketterson 1982).

The magnitude of the disparity in migration mortality that would be necessary to equalize

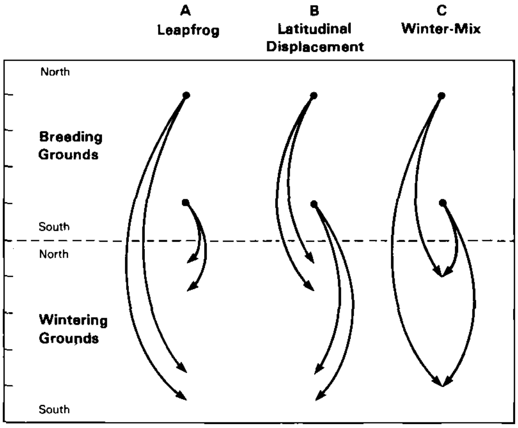

Fig. 4. Three possible migration patterns in the Dark-eyed Junco: leapfrog, latitudinal displacement, and winter-mix. Two breeding populations, each consisting of males and females making long- and short-distance migrations to their wintering sites, are shown for each pattern. Hatching on lefthand vertical axis indicates arbitrary units of distance. The predicted consequences of the patterns are summarized in Table 6.

annual survival is easy to overestimate if one thinks only in terms of the overall annual rate. As an example, consider two adult populations of equal size leaving the same breeding ground, one heading for a northern winter site and the other for a southern. In order to reduce each by 50% at the start of the next fall migration and to impose on the northern population a winter mortality rate twice as great as that of the southern population, seasonal mortality rates during the year could be as follows: northern population—fall migration, 13%; winter, 30%; spring migration, 13%; breeding season, 5%; southern population—fall migration, 21%; winter, 15%; spring migration, 21%; breeding season, 5%.

Consequences of patterns of migration.—To this point, consideration has been virtually confined to winter junco populations and to why and how we believe these probably arrive at equal survivorship, on average, from December to December. Breeding populations have been referred to only when necessary to project the effects that various mortality patterns might have on sex ratio or the mating system. These expected effects would be independent of the latitude of the breeding site. But breeding latitude will have important consequences if we are correct in proposing that migration mortality is positively correlated with distance migrated, and we now deal with that aspect of the subject. The question is whether the model for winter populations—equal annual mortality rates and therefore no need to suppose unequal reproduction—suffices for breeding populations or must be modified to permit variation in reproduction among these. The answer, we think, depends on what migration pattern (defined below) has evolved in the junco.

Figure 4 depicts three basic ways (hereafter patterns) in which breeding populations can arrange themselves on the wintering grounds. (Intermediate patterns can be imagined, but consideration of them would add nothing to this analysis.) In the leapfrog pattern (Greenberg 1980) (A), the southernmost breeders make the shortest migration and therefore winter farthest north, etc., and populations from different latitudes do not intermingle in the winter range. In the latitudinal displacement pattern (B), all breeding populations travel the same distance; the northernmost breeders are the northernmost winterers, and here again breeding populations remain intact in the winter range. In the winter-mix pattern (C), no relationship exists between latitudes of breeding and of wintering sites, and breeding populations mingle randomly in winter.

Before predicting the different consequences these patterns would have for the dynamics and other characteristics of junco populations, we state those respects in which we assume all patterns will be alike: (1) members of breeding and winter populations have equal average fitness; (2) females from each breeding population tend to winter south of males from the same population; (3) because migration mortality and winter survivorship correlate positively with distance migrated and can offset each other, southern winterers from each breeding population are equal in fitness with northern winterers from that population; (4) breeding-season mortality does not vary clinally with latitude. (This last assumption can be discarded with predictable consequences, but we see no reason to complicate matters by doing so here.)

Table 6 presents consequences we expect each pattern to produce. In A, the southern breeding population migrates the shortest distance and trades its higher migration survivorship for higher winter mortality; equal fit-

TABLE 6. Predicted consequences of possible migration patterns in juncos, based on the conclusion that migration mortality increases with distance traveled, while winter mortality decreases.

	Migratory pattern of breeding populations		
	A Leapfrog	B Latitudinal displacement	C Winter-mix
Northern vs. southern breeding populations[a]			
Annual mortality	=	$\neq$, N > S	$\neq$, N > S
Migration mortality	$\neq$, N > S	=	$\neq$, N > S
Winter mortality	$\neq$, S > N	$\neq$, N > S	=
Reproductive success	=	$\neq$, N > S	$\neq$, N > S
Northern vs. southern winter populations[a]			
Annual mortality	=	$\neq$, N > S	=
Migration mortality	$\neq$, S > N	=	$\neq$, S > N
Winter mortality	$\neq$, N > S	$\neq$, N > S	$\neq$, N > S
Reproductive success	=	$\neq$, N > S	=
Variance in genetically based characters greater in winter than in breeding populations?	No	No	Yes
Preserves during winter any clinal variation occurring on breeding grounds?	Yes (but cline reversed)	Yes (and cline in same direction)	No

[a] N = northern; S = southern.

ness across populations (both winter and summer) can be achieved without inequality of reproduction. In B, migration mortality is equal for all populations, but winter mortality of northern breeders is higher; these must have higher reproduction if they are to be as fit as southern breeders. Because C mixes northern and southern breeders on the wintering ground, winter mortality is invariant with breeding latitude, but northern breeders make longer migrations, die at a higher rate for that reason, and must have greater productivity if their fitness is to equal that of southern breeders.

Each pattern predicts its own set of characteristics of winter populations, and these can be compared with what is known to date about wintering juncos. Annual survival rates measured from December to December (i.e. at start of winter) could be equal under A but not under B. They could also be equal under C, but the situation would be somewhat complex: equality across winter populations would exist despite inequality across breeding populations. Restated in terms of fitness, the equal average fitness of members of winter populations would be attained because each population would consist of two elements: (1) southern breeders with lower migration mortality and lower reproduction, and (2) northern breeders with higher migration mortality and higher reproduction. As for winter sex ratios, in our view only a migration that incorporated some degree of pattern C would produce clinal variation. Finally, to the extent that breeding populations vary morphologically (Miller 1941: 317 describes some geographical variation in *Junco h. hyemalis*), A and B would preserve such variation in the winter range, whereas C would tend to abolish it. Variance in relevant morphological characters of winter populations (or in other genetically based traits) would in that case be greater than that of breeding populations under C but not under the other two patterns.

It will be apparent that if the junco satisfies the assumptions set forth above, its partial sexual segregation in winter suggests that its migration pattern approaches C more closely than A or B. The evidence favoring equal annual mortality from December to December is consistent with C but also with A. Our body-size data for winter and summer populations are still being analyzed, but we can state now that if there are latitudinal body-size clines in summer they are not preserved in winter.

In conclusion, it is obvious that adequate breeding studies in northern and southern Canada, although they would be difficult to carry out, would reveal whether reproductive success varies with latitude and would thus contribute to an understanding of the junco's migration pattern.

THE ROLE OF MIGRATION IN LIFE HISTORY

How do our evidence and interpretations relate to current theory concerning the significance of migration for individual fitness? Most consideration of variation in distance migrated by conspecifics has approached the problem from the point of view of breeding populations. In particular, the question has been the identification of the advantages and disadvantages of remaining on the breeding ground throughout the year among so-called partially migratory species. The logic of theories about systems in which fewer than all individuals are migratory, however, appears applicable also to fully migratory species in which elements of the population travel varying distances and therefore settle in different winter sites.

Baker (1978: 635) summarizes the literature on partial migrants and derives two models to account for the fact that selection has not eliminated either the migrant or the nonmigrant element. The models are alike in assuming (1) a stable system (i.e. equal fitness for migrants and nonmigrants), in which (2) the nonmigrant element in some or all years suffers higher winter mortality than the migrant (3) as the result of failure to leave the breeding range. One model proposes that a higher reproductive rate compensates for the greater winter mortality of nonmigrants and attributes this reproductive gain to priority of access to limiting breeding resources (von Haartman 1968) or to a longer period in which to reproduce. [Compare Nolan (1978) on the advantages in terms of breeding time gained by male Prairie Warblers that return early to the breeding ground, and see Greenberg (1980), who argues that temperate-zone breeding species wintering in the tropics pay for enjoying a benign winter climate by losing time for reproduction.] This view, as we read it, does not concern itself with mortality associated with migration, assumes that the benefits of migrating are self-evident, and considers the theoretical problem to be accounting for the continued existence of the nonmigrants. The other model is that of Lack (1954, 1968b), who starts from the proposition that migration is costly. In some years migration mortality is higher than the winter mortality of sedentary individuals, in other years lower. Over time, the annual rates for migrants and nonmigrants balance out, and both elements continue to exist. Productivity apparently is taken as unvarying with migratory status.

Lack's view, because it weighs migration losses against winter losses, resembles the model proposed herein for winter junco populations. It differs, however, in that its concern is with unequal year-to-year mortality rates that fluctuate around equal long-term means. We do not disagree with Lack, in that we do not suppose that the annual mortality rates of northern- and southern-wintering juncos are identical from year to year, although in theory annual rates could be invariant despite large and important differences in their seasonal components. Nevertheless, it seems clearly desirable to analyze population dynamics over the shortest possible, biologically meaningful time intervals, even though other temporal perspectives may be equally important. With special reference to the subject of this paper, study of geographic differences in winter mortality of conspecific populations may permit estimates of the scale of mortality during migration if annual and breeding-season survivorships of the populations are known.

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The American Ornithologists' Union will hold its annual meeting in Chicago, Illinois from **10–14 October 1982.** A formal call for papers is enclosed with this issue of *The Auk,* with a deadline for submission of abstracts for papers and poster sessions of **20 May 1982.** For further information on the scientific program, contact **James R. Karr, Program Chairman, Department of Ecology, Ethology, and Evolution, University of Illinois, 606 E. Healey, Champaign, Illinois 61820 USA.**

COMMUNITY ORGANIZATION OF RIPARIAN BREEDING BIRDS: RESPONSE TO AN ANNUAL RESOURCE PEAK

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ABSTRACT.—Spatial distribution, foraging behavior, and diets of 12–13 insectivorous bird species were measured during two breeding seasons in a cottonwood- and willow-dominated riparian forest in Arizona. Spatially, no negative associations existed between any species in either year. Although foraging behavior varied considerably, diets overlapped broadly, even between members of different foraging guilds. Eight species preyed heavily on cicadas (38–80% of diet). Sampling of emerging cicadas in cottonwood-willow habitat indicated that numbers exceeded the metabolic needs of the bird community by as much as tenfold. Peak cicada numbers coincided with fledging young in all eight species. We propose that this seasonally superabundant and predictable resource permits coexistence without niche segregation and may, in part, explain the high density and diversity of ecologically similar breeding birds in desert riparian communities. It appears that niche variables such as bill shape and foraging behavior may not be true predictors of actual resource use within a community. Assumptions of resource-based interspecific competition among breeding birds are not supported. *Received 4 May 1981, accepted 1 October 1981.*

AMONG the forces that operate to shape and maintain patterns of avian community organization, competition for limited resources (e.g. food) has been frequently invoked as a primary selective force (MacArthur 1972, Cody 1974, Cody and Diamond 1975). Such competition has rarely been unequivocally demonstrated for birds. An essential assumption behind competition theory is that resources are in short supply. Although White (1978) argued that all organisms are limited by an inadequate supply of nitrogenous foods, this has not been properly demonstrated for many bird communities. Recently, strong criticism of the application of competition theory in community ecology has been expressed (Wiens 1977, Conner and Simberloff 1979), and older arguments against competition are not resolved (e.g. Andrewartha and Birch 1954).

Measurements of avian diets are lacking in most community studies involving resource use. Instead, diets are most often inferred from morphological (Schoener 1974, Hespenheide 1975) or behavioral measures (MacArthur 1958, Cody 1974, Rabenold 1978). The few studies that have examined actual resource use emphasized the inadequacies of such inferences and have not supported the premises of the competition argument (e.g. Wiens and Rotenberry 1979, Rotenberry 1980a). Furthermore, resource-availability patterns are poorly known in even the most well-studied communities.

In the deserts of western North America, riparian forests (the alluvial floodplain and its attendant vegetation) have been shown to be of great ecological importance to bird populations (Carothers et al. 1974, Anderson and Ohmart 1977, Stamp 1978). These ecosystems typically support extremely high densities and diversities of breeding bird species and provide vegetationally and geographically well-defined systems for study.

Riparian systems, like other temperate forests, undergo marked seasonal changes in primary and secondary productivity. It might be predicted that the avian community present during the period of peak productivity would be structured in part by aspects of that resource peak.

We studied an avian community on a large riparian forest plot over two complete breeding seasons. The general approach of the study was to examine densities, microhabitat preferences, foraging behaviors, and diets of all diurnal insectivorous species on the plot. This report documents a response within this bird community to a summer resource peak and discusses the evolutionary consequences of this response in light of existing community theory.

METHODS

Study area.—A 20-ha plot was established in a continuous forest stand along the Bill Williams River near its delta at Lake Havasu in Yuma County, Arizona, elevation 100 m. The dominant tree species are cottonwood (*Populus fremontii*) and willow (*Salix gooddingii*), with a patchy understory of exotic salt cedar (*Tamarix chinensis*), cattails (*Typha latifolia*), and bulrushes (*Scirpus* spp.). Daily temperature varied from −6°C to 33°C in early spring, and from 8°C to 43°C in summer. Other details are described in Rosenberg (1980).

Density and breeding phenology.—We gridded the 20-ha plot at 20-m intervals with surveyor's tape and marked each grid point with a coordinate number. Detections of all territorial breeding species were recorded on daily field maps from January through July 1977 and February through August 1978. We gave special attention to locating nests, following known pairs, and determining territorial boundaries. All parts of the grid received approximately equal coverage. We determined the number of pairs and the relative territory size from the composite of field maps for each season.

In addition, we assigned each bird detection its closest grid coordinate number from the daily field maps. Totals of 1,482 bird detections in 1977 and 1,800 detections in 1978 of 12 species were used in this analysis. Associations between pairs of bird species were tested separately for each season based on the frequency of co-occurrence at each of the 281 points. The Cramer's V statistic was calculated as:

$$V = \frac{ad - bc}{(mnrs)^{\frac{1}{2}}},$$

where a, b, c, and d are the observed cells of a 2 × 2 contingency table, and m, n, r, and s are the row and column totals, respectively (Pielou 1977: 201). This is essentially a correlation coefficient and its significance was tested by simultaneously computing "χ^2," which approximates a Chi-square distribution with one degree of freedom.

Foraging behavior.—We observed foraging by birds on the study plot and in similar forest stands along the Bill Williams River. A foraging observation was defined as an actual attempt to procure prey, and we recorded the following data for each observation: bird species, foraging method, height of bird in tree, tree species, tree height, branch diameter, portion of tree, substrate from which prey was captured, and type of prey (if observed). All states of foraging measures are listed and defined in the Appendix. A total of 2,122 observations of 12 species was included in this analysis.

Frequencies and proportions of all states of all foraging measures were computed by subprogram CROSSTABS in SPSS (Nie et al. 1975). We present data for the two seasons combined.

The degree of overlap between species pairs (i, j) for each foraging measure was calculated as:

$$O_a = \frac{\Sigma\, p_{ia} p_{ja}}{(\Sigma\, p^2_{ia})(\Sigma\, p^2_{ja})},$$

where p_{ia} and p_{ja} are the proportional use of resource state "a" by species i and j, respectively (Pianka 1974, May 1975).

To assess the combined effects of overlap in several foraging measures, two additional matrices were computed. The first represents the total overlap in foraging behavior and is the average of overlaps for each species pair in foraging method, substrate, and branch diameter. Because these measures were reasoned to be correlated, the summation-alpha approach (Cody 1974) appeared satisfactory. Similarly, the second matrix represents the total overlap in foraging space and is the average of overlaps in use of tree species and tree portion multiplied by the overlap in foraging height. The use of product-alpha (Cody 1974) seemed appropriate in the case of foraging height, because this measure introduced conditions that were independent of other space measures, i.e. two species that did not overlap in foraging height could not overlap in overall foraging space. The hazards of this approach were discussed by May (1975), but these matrices seemed to represent a realistic approximation of the patterns of similarity within this bird community. We performed a group average clustering on these matrices to construct dendrograms for visual display (Cody 1974).

To test for actual differences between species for each foraging measure, we compared the distributions of the state frequencies of each measure for goodness-of-fit using G_H (Sokal and Rohlf 1969: 575). The lack of a significant difference between two species is assumed to imply a biologically important overlap. When the statistical significances associated with different degrees of overlap between species are compared directly, the biological relevance of each approach can be assessed.

Diet/morphology.—During July and August 1978, 106 birds of 13 species were collected from riparian forest stands similar to the study plot, and their esophagi and stomachs were immediately preserved in a formalin solution. We recorded age, sex, weight, bill size (exposed culmen, depth, and width), wing chord, fat condition, and condition of molt for each specimen. A reference series of skins was prepared.

Esophageal and stomach contents were dried and weighed, and their volumes determined. Length, frequency, and percent-volume of each individual prey item were recorded. All arthropod prey were identified to order and many were identified to family. Identifiable insect parts contributed to the percent-volume of that category but not to its frequency.

TABLE 1. Densities and breeding characteristics of 13 species of birds on a riparian forest plot. Species names are followed by abbreviations used in subsequent tables and figures. Density is based on estimates from two breeding seasons. Solid line indicates duration of stay; F indicates timing of fledging of broods.

			Breeding chronology							
Species	Code	Density (*n*/40 ha)	January	February	March	April	May	June	July	August
Yellow-billed Cuckoo (*Coccyzus americanus*)	YC	28–30					—	—	F	—
Common Flicker (*Colaptes auratus*)	CF	2–4	—	—	—	—	F	—	F	—
Gila Woodpecker (*Melanerpes uropygialis*)	GW	36–40	—	—	—	—	F	—	F	—
Ladder-backed Woodpecker (*Picoides scalaris*)	LW	28–36	—	—	—	—	F	—	—	—
Wied's Crested Flycatcher (*Myiarchus tyrannulus*)	WF	20–24					—	F	—	—
Ash-throated Flycatcher (*Myiarchus cinerascens*)	AF	4–6			—	—	F	—	F	—
Verdin (*Auriparus flaviceps*)	VN	20–24	- -	- -	- -	—	—	F	F	—
Common Yellowthroat (*Geothlypis trichas*)	YT	80				—	—	F	F	—
Northern Oriole (*Icterus galbula*)	NO	64–80		—	—	—	F	F	F	—
Summer Tanager (*Piranga rubra*)	ST	24				—	—	—	F F	—
Blue Grosbeak (*Guiraca caerulea*)	BG	4				—	—	—	F	—
Abert's Towhee (*Pipilo aberti*)	AT	50–56	—	—	F	F	—	F	F	—
Song Sparrow (*Melospiza melodia*)	SS	80–100	—	—	—	F	—	—	F	—

Unidentified parts were not included in volumetric analysis.

The importance of selecting relevant categorical divisions in the computation of diet diversity and overlaps has been emphasized by Hespenheide (1975) and others. Because a majority of insect orders shows consistent features of form, habit, and catchability, this level was used in most cases to group prey items in this study. A few families (e.g. Cicadidae), which were frequently identified and were considered sufficiently different from others in their order, comprised distinct categories. We considered soft-bodied larvae of several orders as one group and all spiders as another. Overlap matrices were prepared for all species pairs, as described. We also grouped prey items into 10-mm size classes for computation of prey size overlaps, as above. The G_H statistic was used to test for differences in the mean prey-size and prey-taxa frequency distributions of each species pair, as was done for foraging measures. Percent-volume data were not appropriate for such comparisons.

From the morphological measurements, the ratio of the values of each measure for any pair of species was used as an index of similarity. Overall morphological similarity for each species pair was the average of the similarity values for each measure. We performed group average clustering on the matrix of similarity values, as for foraging overlaps.

RESULTS

Density amd breeding phenology.—Table 1 lists the breeding densities (*n*/40 ha) and summarizes the breeding biology for the 13 species in this study. Densities were nearly identical

TABLE 2. Summary of spatial associations among 12 riparian bird species in 1977 and 1978. + = significant positive association (Cramer's V; $P < 0.05$); ○ = no association; n = number of grid points where a species occurred each season. Species codes from Table 1.

			1977											
	n		108	152	99	109	22	46	49	136	143	24	25	72
	n	Species	YC	GW	LW	WF	AF	VN	YT	NO	ST	BG	AT	SS
	72	YC		○	○	○	○	○	○	+	○	○	○	○
	144	GW	○		+	+	+	○	○	○	○	+	○	○
	133	LW	○	+		○	○	○	○	○	○	○	○	○
	114	WF	+	+	○		○	+	+	○	○	○	+	○
1	38	AF	○	○	○	○		+	○	○	○	○	○	○
9	32	VN	○	○	○	○	+		○	○	○	○	○	○
7	93	YT	+	+	+	○	○	○		○	+	○	○	○
8	148	NO	○	+	+	+	○	○	+		○	○	○	○
	95	ST	+	○	○	○	○	○	+	○		○	○	○
	11	BG	○	○	○	○	○	○	○	○	○		○	○
	84	AT	○	○	○	○	○	○	○	+	○	○		○
	136	SS	○	○	○	+	○	○	○	+	○	○	○	

in both seasons and are presented as a range of values, representing breeding adults. Five species were permanent residents on the plot. The Verdin (*Auriparus flaviceps*) is a resident in the region but was only a summer visitor to the study area. All species except the Common Flicker (*Colaptes auratus*) nested on the plot. Flickers used saguaro cacti (*Carnegiea gigantea*) in the adjacent desert for nesting but regularly foraged in the riparian forest. This species, however, was not detected frequently enough on the plot to be included in the spatial analysis.

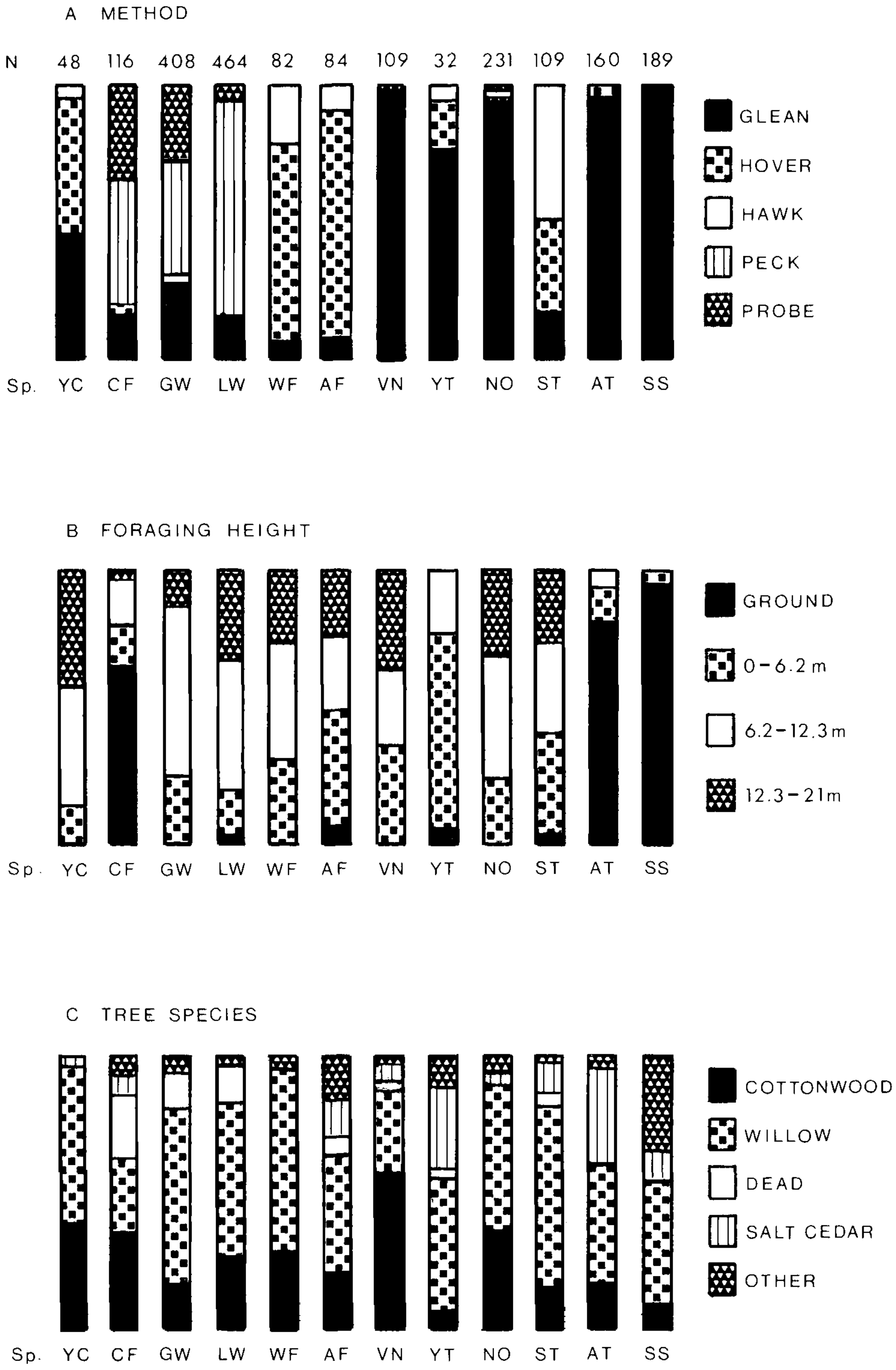
If bird species were dividing space so that they were avoiding or in some way excluding one another, species pairs should have occurred together less frequently than by chance in a given season. No significant negative associations were found for any species pair in either year (Table 2). Nine significant positive associations were found in 1977, however, and 16 in 1978. With 66 comparisons, as many as four positive and four negative associations would be expected if the species were distributed at random with respect to one another (Kirk 1968: 197). It can be concluded, then, that there was a tendency for some species such as cavity nesters to be clumped together on the plot, although the pattern of positive association was not consistent.

Foraging behavior.—Species-specific use patterns for each foraging measure are illustrated in Fig. 1. Qualitatively, three major functional groupings of species were recognized. These groups may be termed foraging guilds (Root 1967).

The two species of woodpeckers foraged primarily on bark, on larger branches (e.g. trunks), and in the inner portion of trees. Abert's Towhees (*Pipilo aberti*) and Song Sparrows (*Melospiza melodia*) foraged on the ground. The Common Flicker foraged primarily like other woodpeckers, but it also fed on the ground.

The remaining seven species can be generally grouped into a canopy-feeding guild. All tended to use leaves as a substrate and to feed on the outer portions of trees. This group can be divided further into specialist gleaners [Verdin, Common Yellowthroat (*Geothlypis trichas*), and Northern Oriole (*Icterus galbula*)] and those that tend to hover or hawk for prey [Yellow-billed Cuckoo (*Coccyzus americanus*), two flycatchers, and Summer Tanager (*Piranga rubra*)]. Sufficient foraging data for the Blue Grosbeak (*Guiraca caerulea*) were not obtained. Anecdotal observations, however, suggest that this species also hovered and gleaned from foliage.

Average niche overlaps and their associated levels of statistical significance between all species pairs for each measure were presented by Rosenberg (1980). A summary of these relationships is presented in Table 3. In general,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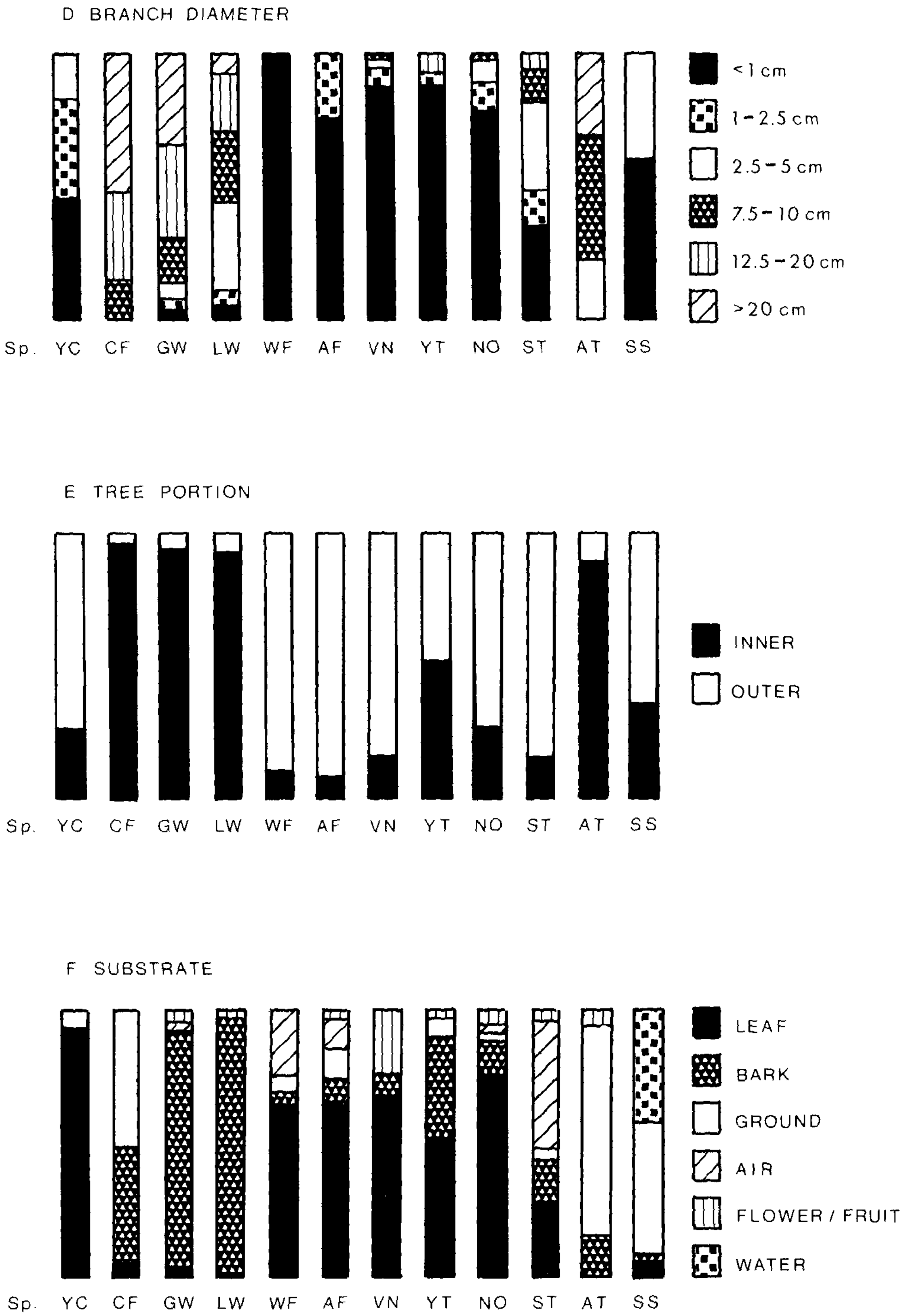

Fig. 1. Foraging behavior of 12 riparian birds for six measures (A–F). Bars indicate percentage of observations. Sample size (N) applies to all measures. Species codes from Table 1.

TABLE 3. A demonstration of the lack of significant differences among 12 riparian birds on three measures of foraging behavior (above diagonal) and three measures of foraging space (below diagonal). M = method, B = branch size, S = substrate, H = height, T = tree species, P = tree portion. Species codes from Table 1.

Species	YC	CF	GW	LW	WF	AF	VN	YT	NO	ST	AT	SS
YC		—	—	—	BS-	BS-	S—	BS-	BS-	B—	—	—[a]
CF	—		MB-	—	—	—	—	—	—	—	—	—
GW	—	P—		S—	—	—	—	—	—	—	—	—
LW	HT-	P—	HTP		—	—	—	—	—	—	—	—
WF	HTP	—	H—	H—		MBS	B—	B—	B—	—	—	—
AF	P—	—	—	—	HP-		B—	B—	BS-	—	—	—
VN	HTP	—	—	—	HP-	HP-		MB-	MBS	—	M—	M—
YT	P—	—	—	—	—	HT-	P—		MBS	—	M—	M—
NO	HTP	—	H—	H—	HTP	HP-	HP-	P—		—	M—	M—
ST	HTP	—	—	H—	HTP	HTP	HP-	P—	HTP		—	—
AT	—	HP-	P—	P—	—	—	—	T—	—	—		M—
SS	P—	—	—	—	P—	P—	P—	P—	P—	P—	H—	

[a] Song Sparrows rarely used branches; their use of this measure was not tested.

pairs with the highest calculated overlaps in each matrix (usually >0.900) did not differ significantly. All differences stated below were significant ($P < 0.05$).

As described, overlap matrices for the six foraging measures were combined into two sets of overlap patterns: one for foraging behavior and one for foraging space (Fig. 2). In general, the clustering of species paralleled the previous separation into three guilds, although membership by several species was now less clear.

Behaviorally, the most similar species were within the canopy-feeding guild. The two congeneric flycatchers were statistically inseparable in all three behavioral measures. Both fed primarily by snatching insects from foliage during short flights through the canopy. The Northern Oriole, Verdin, and Common Yellowthroat were specialist leafgleaners and did not differ in eight of nine possible comparisons. The Yellow-billed Cuckoo was intermediate in behavior between these two groups, whereas the Summer Tanager differed from all species except the cuckoo on all measures.

The Gila (*Melanerpes uropygialis*) and Ladder-backed woodpeckers (*Picoides scalaris*) were similar only in their use of bark as a substrate; they differed with respect to foraging method and branch size. The Common Flicker differed from the Ladder-backed Woodpecker in all measures but differed from the Gila Woodpecker only with respect to substrate. The two ground foragers used identical foraging methods but used different substrates; the Song Sparrow often gleaned insects from the surface of shallow standing water, whereas the Abert's Towhee gleaned from dry ground and litter.

With respect to foraging space, again the greatest overlap was within the canopy-feeding guild. The Northern Oriole, Wied's Crested Flycatcher (*Myiarchus tyrannulus*), and Yellow-billed Cuckoo did not differ in any spatial measure. The Verdin and Summer Tanager differed only in regard to tree species use. The two flycatchers overlapped less spatially than behaviorally, with the Ash-throated Flycatcher (*Myiarchus cinerascens*) foraging more in salt cedar. Overall, there were fewer differences in spatial than in behavioral measures within this guild (43 versus 29), and there was a nonsignificant tendency for these to be complementary ($r = -0.323$, $P \gg 0.05$). The Common Yellowthroat was widely separated spatially from the other foliage feeders and from all other species as well.

The two woodpeckers were inseparable in all spatial measures. The Common Flicker's foraging space was most similar to the Abert's Towhee's, with no differences in foraging height or use of the inner portion of trees. The Song Sparrow and Abert's Towhee did not differ in foraging-height distributions and were widely separated from most other species.

Morphology.—Table 4 lists the means and standard deviations of all morphological measures for the 13 species used in this study. The

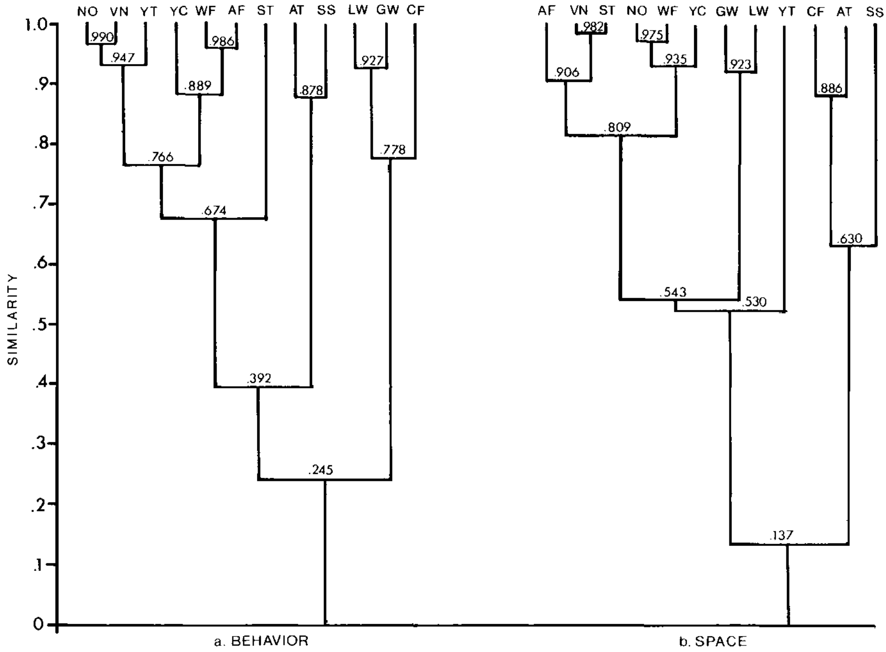

Fig. 2. Foraging similarity among 12 riparian birds. Behavior (a) = average of overlaps in method, branch size, and substrate. Space (b) = average of overlaps in tree species and tree portion multiplied by overlap in height (see text). Species codes from Table 1.

smallest species was the Verdin (6.5 g, 8.4-mm bill length), and the largest was the Common Flicker (110 g, 32.7-mm bill). Seven species were between 27 and 46 g, with bill lengths varying from 15.7 mm to 23.8 mm.

Overall morphological similarity based on ratios of the measures is illustrated in Fig. 3. In general, species were arrayed by body size and bill length, forming three major size groups. The seven medium-sized species dif-

TABLE 4. Morphological means of 13 species of riparian birds. Standard deviations are in parentheses. Bill length is exposed culmen; width and depth measured at nares. Species codes from Table 1.

				Bill		
Species	*n*	Weight (g)	Wing (mm)	Length (mm)	Width (mm)	Depth (mm)
YC	6	66 (4.8)	149 (4.0)	29.3 (0.9)	7.8 (0.3)	8.9 (0.8)
CF	2	110 (2.6)	145 (3.1)	32.7 (2.7)	9.2 (0.1)	8.0 (0.3)
GW	11	62 (6.9)	128 (1.8)	27.4 (2.8)	7.2 (0.6)	7.3 (0.5)
LW	2	33 (3.0)	106 (8.5)	20.4 (0.6)	6.5 (0.2)	5.9 (0.2)
WF	11	38 (11.6)	108 (5.8)	23.8 (2.5)	9.7 (0.6)	8.1 (0.6)
AF	13	27 (1.8)	93 (3.4)	19.0 (0.7)	7.5 (0.4)	6.3 (0.3)
VN	12	6.5 (0.4)	49 (3.1)	8.4 (0.4)	3.7 (0.4)	3.9 (0.4)
YT	10	10 (0.7)	54 (1.3)	11.9 (0.7)	3.6 (0.3)	3.6 (0.4)
NO	10	31 (2.7)	95 (3.0)	18.1 (0.5)	5.7 (0.5)	6.9 (0.4)
ST	7	33 (3.3)	100 (3.7)	20.3 (0.8)	9.4 (0.4)	9.7 (0.4)
BG	9	27 (1.9)	85 (3.6)	16.3 (0.9)	8.5 (0.8)	11.3 (0.8)
AT	10	46 (3.8)	89 (2.8)	15.7 (0.4)	6.7 (0.5)	8.8 (0.4)
SS	10	19 (2.4)	64 (2.1)	11.9 (0.5)	5.4 (0.4)	6.2 (0.3)

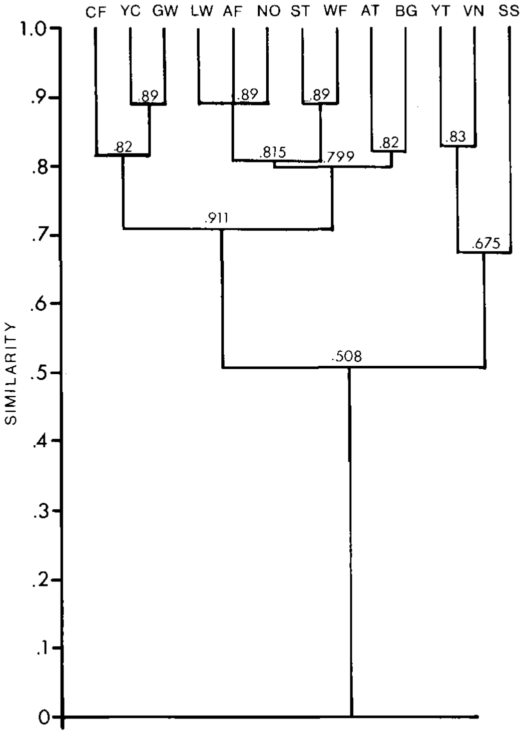

Fig. 3. Morphological similarity among 13 riparian birds. Represents average of ratios of five measures for each species pair (Table 4). Species codes from Table 1.

fered primarily with respect to bill width and depth. The Ladder-backed Woodpecker, Northern Oriole, and Ash-throated Flycatcher had relatively narrow or flattened bills; the Wied's Crested Flycatcher and Summer Tanager had the widest bills, and the Abert's Towhee and Blue Grosbeak had very deep as well as wide bills.

Diet.—Contents of 106 stomachs, representing midsummer diets of 13 species, were used for this study. The small sample size for the Common Flicker and Ladder-backed Woodpecker prevents conclusive analysis; they were included for completeness, however.

Distribution of size classes in the diets is shown in Fig. 4. The largest and smallest species (Common Flicker and Verdin) were specialists on the smallest size class, illustrating the danger of inferring prey size indirectly from bill measurements. The most frequently eaten size class among the larger species was 21–30 mm. All these species, except the Yellow-billed Cuckoo, ate very small insects as well.

There was much overlap among both the larger and smaller bird species with respect to prey size (Fig. 5a). Within each group, the canopy-foraging summer visitors were nearly inseparable statistically (Table 5). Among permanent residents and the other two foraging guilds, the only nonsignificant difference was between the Gila Woodpecker and the Abert's Towhee.

Distribution of prey types in the diets of the 13 species is shown in Fig. 6. Eight species preyed heavily on cicadas. Among these birds, grasshoppers were an important food for the Yellow-billed Cuckoo, Blue Grosbeak, Abert's Towhee, and possibly the Northern Oriole. Summer Tanagers were the only birds to feed on bees and wasps, and Gila Woodpeckers ate many ants. Abert's Towhees fed heavily on beetles, and the two flycatchers took a wide variety of food items in addition to cicadas.

The smaller bird species fed on a variety of soft-bodied prey, primarily spiders and larvae of several insect orders. The small samples of Common Flicker and Ladder-backed Woodpecker stomachs suggest that their diets may have been very different from most other species. Of the three species sometimes referred to as granivores, the Song Sparrow and Abert's Towhee ate very few seeds, and the nine stomachs of Blue Grosbeaks contained none.

Overlaps in diet are illustrated in Fig. 5b for percent-frequency distributions. Among the eight species that preyed upon cicadas, 23 of 28 pairs did not differ significantly in diet (Table 5). Among the remaining five species, only two of 10 species pairs were different: the Verdin with both the Common Yellowthroat and Song Sparrow.

DISCUSSION

Species usage patterns indicated a high degree of overlap with respect to both space and food. Although diet samples were small, these are believed to be adequate for most species, based on the small variation in individual diets and their correspondence with field observations. Wiens and Rotenberry (1979) similarly justified small samples as being reasonable inventories of avian diets.

The failure of avian species to avoid or ex-

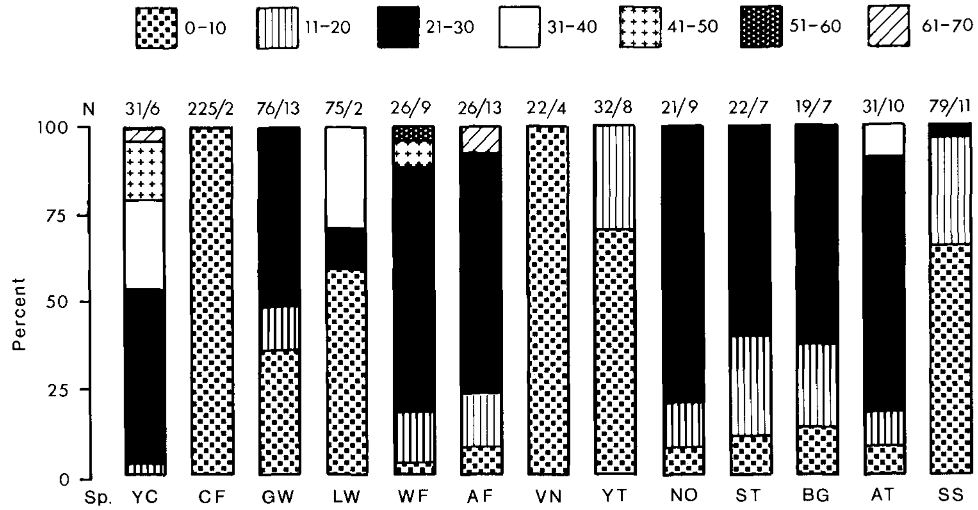

Fig. 4. Prey size distributions of 13 riparian birds. N represents number of food items/number of stomachs. Species codes from Table 1.

clude one another spatially suggests that, for each species, microhabitat selection on the study plot was independent of the other species present. The lack of distinct microhabitat preferences among these species (Rosenberg et al. MS) further suggests that spatial partitioning was unnecessary. An assumption of interspecific competition is not necessary to explain the observed spatial distribution.

In nearly every study investigating actual resource use among a community of breeding birds, a high level of dietary overlap has been

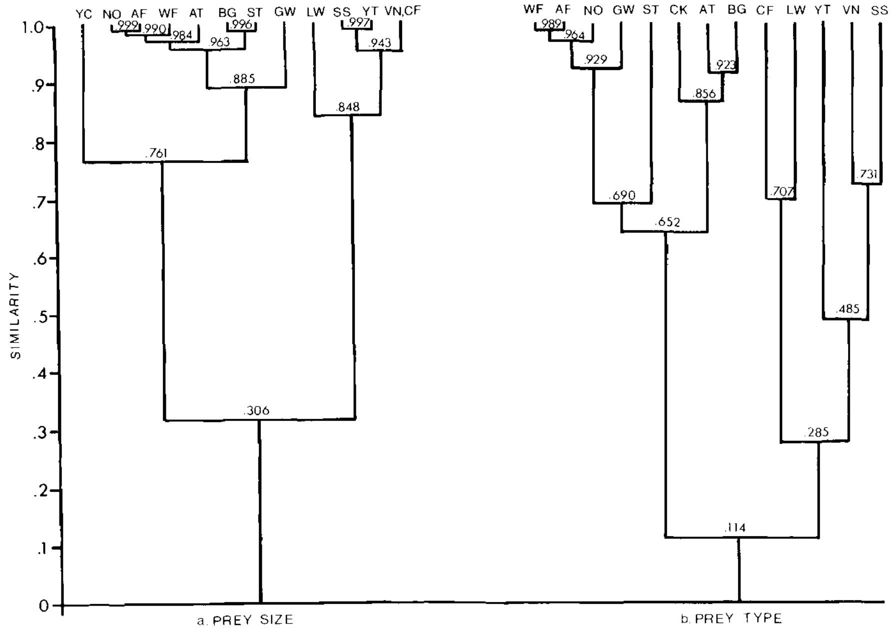

Fig. 5. Similarity in prey size (a) and diet (b) among 13 riparian birds. Overlaps based on percent-frequency distributions. Species codes from Table 1.

TABLE 5. Nonsignificant differences in prey size (S) and prey type (T) among 13 riparian birds. Species codes from Table 1.

Species	YC	CF	GW	LW	WF	AF	VN	YT	NO	ST	BG	AT	SS
YC		—	—	—	S	—	—	—	—	—	—	—	—
CF	—		—	—	—	—	S	—	—	—	—	—	—
GW	—	—		—	—	S	—	—	S	—	S	S	—
LW	—	—	—		—	—	S	—	—	—	—	—	—
WF	T	—	T	—		S	—	—	S	S	S	S	—
AF	—	—	T	—	T		—	—	S	S	S	S	—
VN	—	—	—	—	—	—		S	—	—	—	—	S
YT	—	—	—	—	—	—	T		—	—	—	—	S
NO	T	—	T	—	T	T	—	—		S	S	S	—
ST	T	—	—	—	T	T	—	—	T		S	S	—
BG	T	—	—	—	T	T	—	—	T	T		S	—
AT	T	—	—	—	T	T	—	—	T	T	T		—
SS	—	—	—	—	—	—	T	—	—	—	—	—	

discovered. This is true for such diverse groups as shorebirds (Holmes and Pitelka 1968), blackbirds (Orians and Horn 1969), finches (Pulliam and Enders 1971), owls (Herrera and Hiraldo 1976), grassland insectivores (Wiens and Rotenberry 1979), and riparian insectivores (this study). These findings are in contrast to theoretical predictions of resource allocation and limiting similarity and would most likely be considered exceptions to the "general rule" by these models. As pointed out by Wiens (1977), however, there is no justification in assuming a priori that resource-based competition exists or even that a community is at equilibrium with respect to resource use.

It is often suggested that high dietary overlap, especially among breeding birds, most often results from temporary superabundances of food. The magnitude and duration of these superabundances are rarely measured, however.

Arthropod sweep samples from the study area (Anderson and Ohmart unpubl. data) indicate a peak in biomass and numbers in May. This peak is made up of mostly tiny insects (e.g. Cicadellidae), however, that are apparently unrepresented in the avian diets. Although a July–August peak in larger insects such as Orthopterans can be shown, abundant prey such as Cicadidae, ants, and termites were generally absent from sweep samples.

Because cicadas were so important to a large segment of the bird community, including several similarly sized and potentially competing species, the question of food abundance was addressed using data from Glinski and Ohmart (1981). These consisted of successive weekly counts of cicada exuvia in cottonwood-willow-salt cedar habitat along the San Pedro River in southeastern Arizona in summer 1978. The species of cicada (*Diceroprocta apache*) was the same as on our study plot, and qualitative comparisons of habitat and cicada populations (noise levels) suggest that these data are relevant to the present study.

Cicada numbers peaked at nearly 700,000 per 40 ha on 21 July and declined steadily until late August (Fig. 7). The average number of adult cicadas emerging through the sampling period was 250,000 per 40 ha per week. We feel that these numbers, superimposed on the sweep-sample data, indicate the availability of large insects to birds in midsummer.

Daily expenditures of birds were estimated using the equation $DDE = 11.87\ (\text{mass}^{0.608})$ (Walsberg 1980) for all species that preyed heavily on cicadas (Table 6). The energy needed to maintain this segment of the bird community was estimated as 200,019 kJ per 40 ha per week. Assuming the metabolizable energy from insects to be 4.94 kJ/g (Ricklefs 1974) and using a weight of 1.5 g for a live cicada and a 0.92 efficiency for birds (Thompson and Grant 1968), the energy gained per cicada was calculated as 6.82 kJ. If all these species depended entirely on cicadas for food (a conservative assumption), then approximately 29,328 cicadas were needed each week. This is far fewer than were present in any week during which stomach samples were taken. Because cicadas are conspicuous and easy to catch by a variety of methods, it is reasonable to assume that most

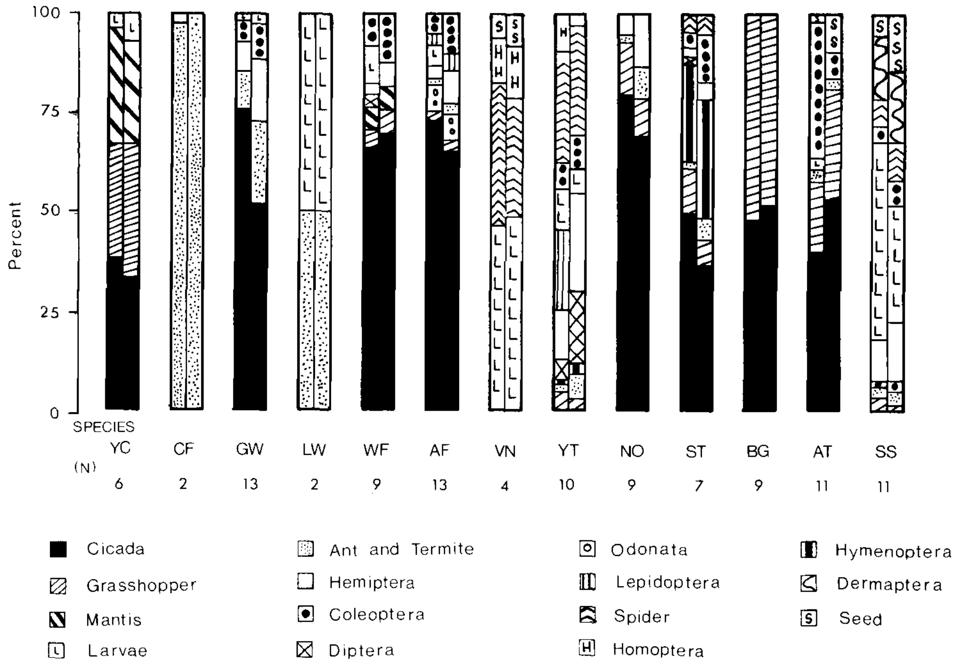

Fig. 6. Diets of 13 riparian birds in summer. Percent-volume on left; percent-frequency on right. Species codes from Table 1.

flying adult cicadas were readily available to birds.

Although the above calculation is crude, and the additional energy demands of growing young need to be considered, the magnitude of the cicada surplus and the additional abundance of grasshoppers and other prey justify the conclusion of a nonlimiting food supply. This is consistent with Rotenberry's (1980b) conclusion from a more complete bioenergetics study of shrubsteppe birds. Furthermore, cicada irruptions are of annual occurrence in this region, suggesting that this surplus is predictable.

All species exploiting cicadas fledged either their first or second broods in July when food was potentially most abundant. This is indirect evidence of a response to a resource peak. In addition, environmental conditions were possibly most stressful at that time, and most other species of the region breed much earlier.

The consequence of this unlimited resource was the convergence in diet of species differing greatly in behavior and morphology. Most striking was the predation on cicadas by Gila Woodpeckers and Abert's Towhees, two species specialized for bark and ground foraging, respectively. These two species could have "avoided competition" with the similar-sized coexisting species but instead shared in the exploitation of the most abundant prey. A similar pattern has been reported for breeding shorebirds differing greatly in body size and bill morphology (Baker 1977).

Thus, measured niche variables such as bill

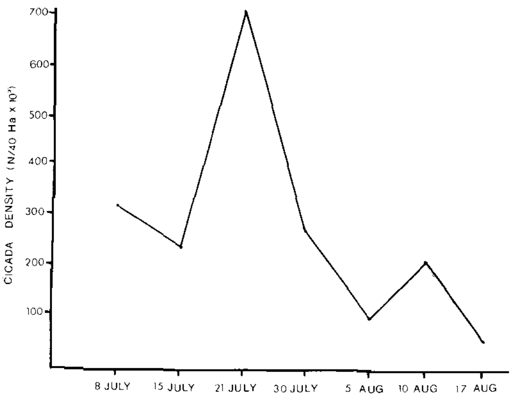

Fig. 7. Density of emerging cicadas in cottonwood-salt cedar habitat during summer 1978. Data from Glinski and Ohmart (1981).

TABLE 6. Energetics of eight medium-sized riparian insectivores. $DEE = 11.87\ \text{mass}^{0.608}$ (Walsberg 1980). Population energy expenditure (PEE) = $DEE \cdot$density. Species codes, densities from Table 1; body mass from Table 4.

Species	*DEE* (kJ/day)	*PEE* (kJ/week/40 ha)
YC	152	30,775
GW	146	38,836
WF	108	16,694
AF	88	3,080
NO	96	46,924
ST	100	16,712
BG	88	1,848
AT	122	45,151
Community		200,019

shape and foraging behavior may not be true predictors of actual resource use within a community, and all community studies that have made such inferences may have drawn spurious conclusions. For example, there is no justification for assuming that coexistence within a community is due to any of the observed differences among the species present. If each individual bird is opportunistically exploiting its environment as efficiently as is necessary to survive and reproduce, irrespective of the presence of other species, then differences may exist within a community, and local interspecific competition need not be invoked as a cause. Indeed such opportunism was implicated by Rotenberry (1980a) as determining relationships among a simple community of arid shrubsteppe birds.

This is not to say that resource limitation and competition could not have been the selection pressures that affected the species-specific differences observed in this and other communities. Selection pressures from competition may only be intermittently important to present-day populations (Wiens 1977). Such selection, however, may still be reflected in current distribution and behavioral repertoires of bird species. The important distinction to be made is between those factors governing the presence of species over large geographic areas through evolutionary time and those that structure short-term, sympatric species interactions.

Until now, we have concentrated heavily on the cicada-eating subset of this community. The remaining smaller species are rather widely separated ecologically, and an apparent peak in small arthropod biomass seems unexploited. In this region, some small insectivores have experienced local extinctions [Yellow Warbler (*Dendroica petechia*), Bell's Vireo (*Vireo bellii*)] or are near the periphery of their breeding range [Bewick's Wren (*Thryomanes bewickii*)]. Thus, this segment of the community is depauperate for reasons probably unrelated to food supply, and discussion of these species can neither refute nor support the above conclusions.

Finally, it should be noted that this discussion has been based only on a period of resource superabundance. Indeed, theory predicts the consequences of such competitive release situations (MacArthur 1972). What is of greater interest is that this may not be a unique or even a rare situation. The evolution of diverse breeding bird communities in response to seasonally superabundant and predictable resources may be quite common, especially in temperate regions. In fact, many communities studied in light of competition models (e.g., MacArthur 1958, Cody 1974) may be examples of such evolution (Rabenold 1978).

Given the abundance and variety of theoretical considerations of community organization, it is clear that empirical evidence lags far behind. Specifically, the exact dietary relationships of species assemblages and the relative seasonal resource productivity of various habitats need to be measured and not inferred. We maintain that such a sound empirical foundation is essential if speculation about community patterns is to be more meaningful.

ACKNOWLEDGMENTS

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APPENDIX. Definitions of foraging measures and states.

Measure	State	Definition
Method	1. Glean	Bird perched; prey captured from surface of substrate
	2. Hover	Bird in flight; prey captured from surface of substrate
	3. Hawk	Both bird and prey in flight
	4. Peck	Bill struck against substrate to expose prey below surface
	5. Probe	Bill enters substrate to capture prey below surface
Foraging height	1. Ground	Ground and litter
	2. 0.0–6.2 m	Understory
	3. 6.2–12.3 m	Mid-canopy
	4. 12.3–21.0 m	Upper-canopy
Tree species	1. Cottonwood	*Populus fremontii*
	2. Willow	*Salix gooddingii*
	3. Dead	Dead cottonwood or willow
	4. Salt cedar	*Tamarix chinensis*
	5. Other	Honey mesquite (*Prosopis glandulosa*), cattails (*Typha latifolia*), etc.
Branch diameter	1. ≤1 cm	
	2. 1.0–2.5 cm	
	3. 2.5–5.0 cm	
	4. 7.5–10.0 cm	
	5. 12.5–20.0 cm	
	6. >20.0 cm	
Tree portion	1. Inner	Larger branches close to and including trunk
	2. Outer	Smaller branches and twigs, containing most foliage
Substrate	1. Leaf	
	2. Bark	
	3. Ground	
	4. Air	
	5. Flower or fruit	
	6. Surface of water	

NESTING ECOLOGY OF ROSEATE SPOONBILLS AT NUECES BAY, TEXAS

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ABSTRACT.—We conducted a study in 1978–1980 of the nesting ecology of Roseate Spoonbills (*Ajaia ajaja*) in a relatively polluted environment at Nueces Bay, Texas. For 154 marked nests, the average clutch size was 3.0 eggs; 73% of the eggs hatched, and 87% of the nests were successful (hatched at least 1 young). The average nest success rate (total fledglings:total eggs) was 50% or 1.5 fledglings per total nests. Incubation began the day after the first egg was laid, and the incubation period for each egg was 22 days. Eggs hatched in the order that they were laid; the first and second eggs hatched on consecutive days, and the second, third, and fourth eggs hatched every other day. Nest composition and size were highly consistent, but nest placement varied considerably and was dependent on the vegetative configuration of the dredge-material islands. Growth rate of nestlings conformed to a "standard" growth curve, where body weight of nestlings at fledging equaled that of adults. There was no difference in weight gain among siblings based on actual age. Nestlings fledged at about 6 weeks of age, when feather development was complete. At fledging, the bills of juveniles had almost reached adult width, but bill length was only 67% that of adults.

In general, environmental pollutants were low (<2 ppm) in spoonbill eggs, though a few eggs contained elevated concentrations of DDE (up to 15 ppm, wet weight). Some eggshells were 5% thinner than those in museum collections, but the degree of thinning was not within the range known to cause population declines. We conclude that organochlorine pollutants are not adversely affecting spoonbill reproduction at Nueces Bay, Texas, though the area is surrounded by industries and agricultural lands. Apparently, spoonbills are less sensitive to these contaminants than are other aquatic species. *Received 8 April 1981, accepted 2 September 1981.*

ALTHOUGH Roseate Spoonbills (*Ajaia ajaja*) probably never were abundant in Texas, they were virtually extirpated there between 1850 and 1919 because of encroaching civilization and exploitation by the millinery trade (Allen 1942). With the advent of laws to protect colonial nesting birds, however, Roseate Spoonbill numbers have gradually increased in Texas to about 2,500 breeding pairs (Blacklock et al. 1979). About 150–200 pairs of spoonbills have nested in Nueces Bay at Corpus Christi, Texas in recent years. In addition, 17 other species of marine and estuarine birds regularly nest there. Nueces Bay is bounded on the south by an industrial complex including oil refineries, chemical plants, and a zinc-smelting plant; other industries and agricultural lands border much of the northern shore. Thus, the potential for pollution problems is great in Nueces Bay because of industrial effluents and pesticide runoff from surrounding crop lands.

Other than the early work of Allen (1942), very little is known of the reproductive biology of Roseate Spoonbills on the Texas Gulf Coast. A preliminary study in 1977 indicated that DDE (the major metabolite of technical DDT) in a few spoonbill eggs from Nueces Bay was within the range known to cause reproductive problems in other avian species (Stickel 1973, 1975). Therefore, we began a 3-yr study in 1978 to learn more of the nesting ecology of Roseate Spoonbills and to evaluate the effects of organochlorine pollutants on reproduction.

METHODS

Our study area in Nueces Bay (27°52′N, 97°30′W) (Fig. 1) consisted of three unnamed dredge-material islands from 1 to 2 ha in size, composed mainly of oyster shell and sand. Low vegetation (<0.5 m), dominated by coast becopa (*Bacopa monnieri*), glasswort (*Salicornia*), and sea oxeye (*Borrichia frutescens*), covered most of each island, and some small (1–3 m)

The Auk 99: 275–284. April 1982

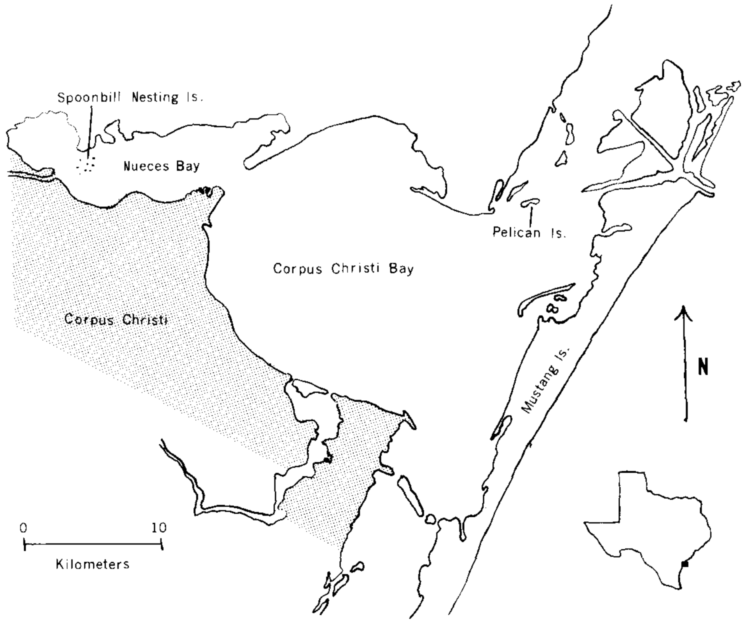

Fig. 1. Roseate Spoonbill study area, Nueces Bay, Texas.

trees and shrubs [retama (*Parkinsonia aculeata*), paloverde (*Cercidium macrum*), saltbush (*Baccharis angustifolia*)] were present on two of them. Associated nesting birds were Great Egrets (*Casmerodius albus*), Snowy Egrets (*Egretta thula*), Cattle Egrets (*Bubulcus ibis*), Great Blue Herons (*Ardea herodias*), Louisiana Herons (*Hydranassa tricolor*), Black-crowned Night Herons (*Nycticorax nycticorax*), and Laughing Gulls (*Larus atricilla*).

In the breeding seasons of 1978–1980 we marked spoonbill nests with numbered stakes at the onset of egglaying; eggs within nests were marked with the assigned nest number and the egg sequence number if known. Nests were visited weekly thereafter, and observations and measurements relating to nesting ecology were recorded. During the week of peak hatching in 1980, we visited nests every other day, except once on 2 consecutive days, to mark hatchlings so that body measurements of known-age nestlings could be recorded throughout the early developmental stage. Body weights were taken with a dietetic scale accurate to ±2 g, and feather development was documented by taking color slides of the various age groups. Our data for feather development from hatching to fledging of known-age spoonbill chicks follow the terminology of Welty (1962).

In 1980 we estimated productivity or nest success (total fledglings : total eggs) on an island adjacent to our study sites in Nueces Bay as a measure of investigator bias. This island was visited only twice. On the first visit (early incubation stage), we counted all nests and the eggs. On the second visit (just before fledging), we counted all the young that were present and the eggs in nests that failed to hatch. Thus, we compared nest success on a relatively undisturbed island with that on the three islands that were visited weekly.

We collected the intact eggs that failed to hatch in our marked nests and one egg each from a series of clutches on islands adjacent to our study sites for organochlorine and lipid analyses. Organochlorine and lipid analyses were conducted at the Patuxent Wildlife Research Center, Laurel, Maryland (1977–1979 samples) and at Raltech Scientific Services, Madison, Wisconsin (1980 samples). A detailed description of Patuxent's analytical methods is included in Cromartie et al. (1975) and Kaiser et al. (1980). Similar analytical procedures were used at Raltech. Residues in 5% of the samples were confirmed by mass spectrometry. Quantification limits were 0.1 ppm for organochlorine pesticides and 0.5 ppm for polychlorinated biphenyls (PCBs) on a wet weight basis. We compared our eggshell thicknesses with those of prepesticide-era eggs from the Texas coast housed at the Welder Wildlife Foundation to determine whether or not shell thinning had occurred. Eggshells we collected were dried at room temperature for at least 30 days, then weighed and measured with the shell membranes intact. Thickness measurements of all eggs were determined with a modified Starrett Model 1010 M micrometer accurate to 0.01 mm. External egg dimensions were measured with calipers, and volumes were estimated following Hoyt (1979).

TABLE 1. Roseate Spoonbill nest measurements, Nueces Bay, Texas.

Parameter	*n*	$\bar{x}$ ± SE	Range
Nest width (cm)	16	55.6 ± 1.8	43–71
Nest depth (cm)	10	10.7 ± 0.3	10–13
Nest height (cm) (atop low vegetation)	28	23.9 ± 2.4	10–51
Nest height (cm) (in trees/shrubs)	12	70.6 ± 13.3	33–168

RESULTS AND DISCUSSION

Nesting chronology.—Adult spoonbills in full breeding plumage began congregating on the Nueces Bay dredge islands around mid-March each year; by late March, 100 or more adults were present. Birds were not paired at this time, and they loafed in large groups on the shores of the islands. By mid-April, several hundred adults were present in the area, and some pairing had occurred. We never saw breeding spoonbills in other than full adult plumage, though Dunstan (1976) reported subadult-plumaged birds nesting in Florida. Rudimentary nests were found on 5 May in 1978, and egglaying began around 20 May; in 1979 and 1980 the average nest building and egglaying dates were 15 April and 25 April.

Allen (1942) estimated the incubation period to be 23–24 days for Texas spoonbills, but he was unsure of the deposition rate and when incubation began. Our data from marked eggs in 29 nests indicate that laying occurred at the rate of one egg every other day, with no variation from this pattern. The time in the nest until hatching was 23 days for the first egg and 22 days for the second, third, and fourth eggs. Because incubation began the day after the first egg was laid, the incubation period for each egg was 22 days. Eggs hatched in the order that they were laid; the first and second eggs hatched on consecutive days, and the hatching interval between the second, third, and fourth eggs was every other day.

By early July, young spoonbills were able to fly several hundred meters to adjacent islands; thus, we estimated that fledging occurred at about 6 weeks of age. By early August, adults and young began to disperse from the islands and by September few birds of any age remained there. We observed small mixed-age flocks of spoonbills in Nueces Bay and other areas of the south Texas coast during the winter months each year, but by mid-October most of the birds had dispersed, presumably southward into Mexico (Allen 1942).

Nest composition and placement.—Spoonbills constructed their nests atop low vegetation and in trees and shrubs with plant material that was abundant on the nesting islands or nearby shoreline. The base of each nest consisted of large dead twigs of saltbush, paloverde, and retama loosely fitted together to form a crude platform about 6 cm deep. Upon this platform, live and dead stems of sea oxeye, saltbush, and grasses (*Paspalum*) were intertwined into a coarse lining about 5 cm deep. The activities of the birds on the nest eventually formed a wide, shallow depression in which the eggs were laid. The external dimensions of nests (width and depth) were consistent, as seen by the small standard errors in Table 1. A brief description of spoonbill nests is given in Bent (1963) and Oberholser (1974), but no mention is made of specific vegetative components or nest measurements. Nest placement on the breeding islands was determined by the vegetative profile; spoonbills nested where low vegetation was most prevalent or in and around trees and shrubs. The height of nests atop low vegetation was much less variable than that of nests in trees and shrubs (Table 1). This was due to the uniform configuration of low vegetation, i.e. density and height, in contrast to the highly variable arrangement of limbs in trees and shrubs.

Nest success.—Clutch size in 1978 was significantly ($P < 0.001$, analysis of variance) lower than in 1979 and 1980 because of fewer 4-egg clutches and more 2-egg clutches in the 1978 sample (Table 2). Six nests (4%) contained 1 egg, 20 (13%) contained 2 eggs, 92 (60%) contained 3 eggs, 34 (22%) contained 4 eggs, and 2 (1%) contained 5 eggs. Allen (1942) recorded a lower average clutch size of 2.6 for a Texas spoonbill colony in 1940, but the proportion of 3-egg clutches in his 1-yr study was identical to ours.

Hatching success varied significantly ($P < 0.02$, Chi-square test) among years, ranging from 58% to 88% (Table 2). The 58% hatching success recorded in 1980 was low when compared to the success rates of the other 2 yr, but there was no difference in hatching success between 1979 and 1980. We were able to account for 92% of the eggs that were laid in 1980. Lowered hatching in 1980 was due main-

TABLE 2. Summary of reproductive success of Roseate Spoonbills at Nueces Bay, Texas, 1978–1980.

Parameter	1978 (n = 72)	1979 (n = 35)	1980 (n = 47)	Total (n = 154)
Clutch size				
Mean	2.8	3.3	3.3	3.0
Mode	3	3	3	3
Range	1–4	1–5	2–5	1–5
Survival rates				
Percentage successful nests[a]	88	97	79	87
Percentage eggs hatched	79	88	58	73
Eggs hatched/nest	2.2	2.9	1.9	2.2
Young to 1 week/nest	2.1	2.7	1.4	2.0
Young to 2 weeks/nest	1.9	2.3	1.3	1.8
Nest success				
Rate (%)[b]	54	52	36	50
Fledglings/total nests	1.5	1.7	1.2	1.5

[a] Percentage nests that hatched at least one young.
[b] Total fledglings/total eggs.

ly to death of embryos during incubation (31%). In 1978 this category accounted for 7% of the egg loss and 1% in 1979. Of the embryonic deaths, 78% occurred in the late stages of development. There was no evidence that the last egg in the clutch contributed more to the overall mortality than earlier eggs, because mortality was evenly divided among eggs of a clutch. The combined proportion of eggs that disappeared and rolled out of nests each year was similar, averaging 13%. Most of the spoonbill pairs were able to hatch at least one young, as evidenced by the high percentage of successful nests for each year (Table 2). There were fewer ($P < 0.005$, Chi-square test) successful nests in 1980 than in the other 2 yr because of lowered hatchability in 1980; no difference ($P > 0.05$) existed between 1978 and 1979. Clutch size had no significant effect ($P > 0.05$, Chi-square test) on the ability of spoonbills to hatch at least one young: 100% of the pairs with 1-egg clutches, 80% with 2-egg clutches, 87% with 3-egg clutches, 88% with 4-egg clutches, and 100% with 5-egg clutches hatched at least one young. In addition, spoonbills having various clutch sizes did not differ significantly ($P > 0.05$) in their ability to raise at least one young to 2 weeks of age: 100% of those with 1 egg, 89% with 2 eggs, 93% with 3 eggs, 87% with 4 eggs, and 100% with 5 eggs had at least one live nestling 2 weeks after hatching.

Total mortality of nestlings from hatching to fledging was 32%, 41%, and 37% for 1978, 1979, and 1980, respectively ($\bar{x}$ = 32%; n = 41). Mortality of nestlings each year was greatest during the first 2 weeks after hatching; 14% of the nestlings were lost during this period in 1978, 21% in 1979, and 32% in 1980 ($\bar{x}$ = 18%, n = 23). Half of the birds that died within the first 2 weeks during the study period were found dead in or near their nests; the other half disappeared between our visits to the colony, and their fate is unknown. Only once did we see evidence of predation; two nests in 1980 contained the partial remains of several hatchlings that appeared to have been removed from the eggs as they were pipping.

Spoonbills fledged fewer ($P < 0.01$, Chi-square test) young in 1980 than in 1978 or 1979 because of lowered hatchability in 1980 (Table 2); there was no difference ($P > 0.05$) in productivity between 1978 and 1979. Though hatchability was lower in 1980, the adults lost only 0.7 young per nest that did hatch; this was identical to the average loss per nest in 1978 but much lower than the 1.2 young per nest that failed to fledge in 1979 (Table 2).

Nest success in 1980 on the island we visited only twice (see Methods) was estimated at 1.3 fledglings per nest (n = 18 nests), similar to the 1.2 fledglings per nest produced in 1980 on our more frequently visited islands. Because there was no difference ($P > 0.05$) in nest success rates between the two areas, our frequent visits to a portion of the breeding colony in 1980 did not appear to impair reproduction.

Growth and development of young.—The Ro-

Table 3. Feather development of known-age Roseate Spoonbill chicks ($n = 10$).

Feather tract	Age (days)							
	1	5	7	9	14	21	35	42
Alar	Down	Primary sheaths emerge				Sheaths rupture		Complete
	Down		Secondary and alula sheaths emerge			Sheaths rupture		Complete
	Down			Tertial and covert sheaths emerge		Sheaths rupture		Complete
Humeral	Down			Sheaths emerge		Sheaths rupture		Complete
Spinal	Down				Central sheaths emerge	Sheaths rupture		Complete
	Down					Lower sheaths emerge and rupture		Complete
	Down					Upper sheaths emerge	Sheaths rupture	Complete
Femoral	Down					Sheaths emerge and rupture		Complete
Crural	Down					Sheaths emerge and rupture		Complete
Caudal	Down					Sheaths emerge and rupture		Complete
Ventral	Down					Sheaths emerge and rupture		Complete
Capital	Down					Sheaths emerge	Sheaths rupture	Complete

Table 4. Bill measurements of known-age Roseate Spoonbill chicks and adult museum specimens.

Age (days)	n	Length (mm)	Cumulative increase (%)	Breadth (mm)[a]	Cumulative increase (%)
1	2	20.0 ± 0.0[b]	12	8.8 ± 0.0	15
9	4	38.5 ± 1.9	23	11.8 ± 0.8	22
12	3	48.3 ± 1.7	28	14.3 ± 0.3	27
16	6	61.6 ± 1.2	36	19.5 ± 0.5	37
17	3	66.0 ± 2.7	39	22.3 ± 0.9	42
19	2	67.0 ± 3.0	39	22.0 ± 1.0	42
39	3	114.3 ± 1.3	67	44.7 ± 0.9	85
56[c]	1	124	73	50	95
Adult[d]	8	170.0 ± 2.4	100	52.7 ± 1.2	100

[a] Breadth measurements were taken at widest part of bill near tip.
[b] $\bar{x}$ ± SE.
[c] Measurements were taken from an individual approximately 8 weeks old found dead on study island in 1980.
[d] Museum specimens at the National Museum of Natural History, Washington, D.C.

seate Spoonbill is a semi-altricial species. The skin, mandibles, and legs of newly hatched chicks are a uniform, deep salmon pink; the feather tracts are covered with thick white down that becomes dry and fluffy about 12 h after hatching, giving the appearance that the entire body is covered with down. About 2 days after hatching, the legs and feet begin to darken, so that by fledging, they generally are a dark gray-brown. The bill remains basically flesh-colored until fledging, though there is a darkening from the mid-bill to the base beginning about 5 days after hatching. The eyes open when the chicks are about 2 days old; at this time the iris is entirely black and remains so until fledging. Our account of eye and bill color in nestlings differs somewhat from that of Allen (1942), who stated that the bills of late nestlings are light yellow and the irises are yellow.

Allen (1942) and Bent (1963) discussed at length plumages and molts in Roseate Spoonbills after fledging, but little attention was given to feather development in nestlings. Sheaths of the flight feathers and their coverts are the first to emerge, beginning around day 5 (Table 3). The rest of the body remains mostly down-covered until about day 21. At this time, the sheaths of the alar tract begin to rupture, and feather sheaths of the other major tracts begin to emerge and rupture. Feather growth continues steadily for the next 3 weeks, and development is complete about 42 days after hatching; birds then are capable of sustained flight and are regarded as fledglings. At fledging, feathers of the alar, humeral, crural, and caudal tracts are light pink; the spinal, femoral, ventral, and capital tracts are white. The tips of the primary feathers are blackish at fledging, first appearing about 28 days after hatching. Roseate Spoonbills do not usually attain full adult plumage until they are 3 yr old, but plumage development may vary widely among individuals (Allen 1942).

The bills of newly hatched spoonbill chicks are not spatulate as in the adults; instead, the chicks have short stubby bills that are soft and leathery. At 9 days of age, the bill near the tip begins to broaden and flatten; at 16 days it begins to take on the characteristic form of the adult. The cumulative increase (% of adult size) in length and breadth is almost identical up to about 19 days of age (Table 4). At 39 days, however, when the birds are near fledging (6 weeks), there is a significant ($P < 0.01$, t-test) bill growth differential; the breadth is 85% of the adults' but the length is only 67%. This growth differential apparently continues after the chicks fledge; the bill of one freshly dead specimen about 8 weeks old had grown to 95% of the adults' in breadth, but to only 73% in length (Table 4).

At hatching, chicks weighed an average of 50 g and gained an average of only 9 g for the next 3 days (Fig. 2); on day 4, however, weight began to increase rapidly. By day 16 the chicks had reached about half the adult weight (Oberholser 1974, J. Remsen pers. comm.). Because nestling weights were not obtained beyond day 19, we estimated the overall growth curve for Roseate Spoonbills using the Gompertz growth equation (Ricklefs 1967). The estimated

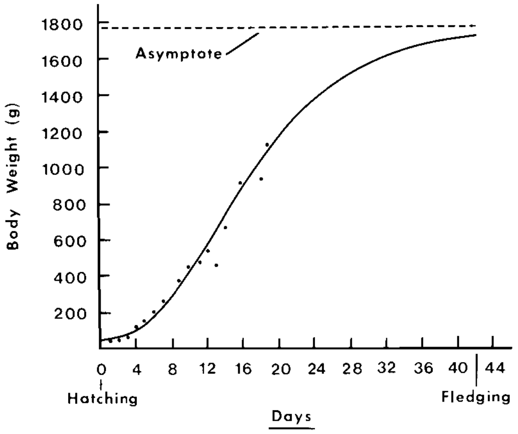

Fig. 2. Growth curve of Roseate Spoonbill nestlings. Some data points represent a single chick, but others may be an average of up to 8.

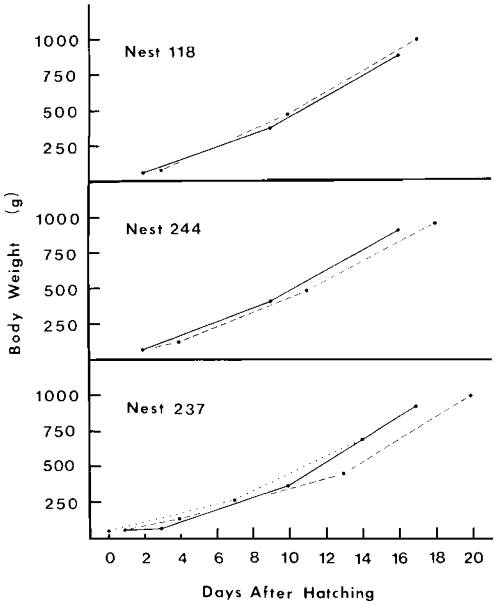

Fig. 3. Weight gain of Roseate Spoonbill siblings from three nests. Dashed, solid, and dotted lines represent first, second, and third chicks, respectively.

asymptote, or fledging weight, closely resembled known adult weight; therefore, the growth curve may be referred to as "standard" (i.e. body weight of nestlings equaled that of adults at fledging: Ricklefs 1968). Initially, there was a weight difference among siblings, as hatching occurred asynchronously; in most instances, however, siblings were visibly indistinguishable in size after about 2½ weeks. Data from known-age siblings in three nests are illustrated in Fig. 3. During develoment, the first chick in nest 118 weighed slightly more than the second chick based on days after hatching, but the reverse was true in nest 244; in nest 237 the third chick weighed slightly more than the others up to about 14 days. Because our growth data on siblings were sparse, we did not attempt a statistical analysis; our limited results suggest, however, that weight gain differences were negligible on an actual age basis. Thus, siblings probably had an equal chance for survival, because fledging weights were similar.

Egg measurements.—Average measurements of Roseate Spoonbill eggs from Nueces Bay, Texas are given in Table 5. Lengths and breadths have been published previously (Bent 1963, Oberholser 1974) and are almost identical to our data. We found no published record, however, of whole weights, volumes, shell weights, or lipid contents of spoonbill eggs. The averages in Table 5 represent measurements of eggs in various stages of development, although most of the eggs were either fresh and unincubated ($n = 33$) or incubated about 5 days or less ($n = 17$). Although there was considerable interclutch variability among some egg parameters, most of the measurements were clustered closely around the means, as evidenced by the extremely small standard errors (Table 5). Variability in whole egg weights was due mainly to water loss during incubation (Ar and Rahn 1980). Fresh eggs averaged 5.5 g heavier than advanced eggs (incubated about 16 days or more), a significant difference ($P < 0.05$, analysis of variance). There was no difference ($P > 0.05$), however, in dry shell weights of fresh and advanced eggs. Percentage lipid showed the greatest variation of the egg parameters measured (Table 5), but there was no difference ($P > 0.05$) in lipid levels of fresh and advanced eggs. There also were no differences ($P > 0.05$) in egg measurements or lipid content among the first, second, third, or fourth eggs ($n = 22$ nests). In all instances there was less variation in egg measurements within clutches than among clutches, indicating that individual females were more inclined to lay eggs of similar

TABLE 5. Measurements of Roseate Spoonbill eggs from Nueces Bay, Texas, 1977–1980.

Parameter	$\bar{x}$ ± SE[a]	Range	Interclutch variability (%)[a]	Intraclutch variability (%)[b]
Length (mm)	64.4 ± 0.3	56.9–71.2	20	13
Breadth (mm)	43.7 ± 0.1	41.3–47.9	14	8
Whole weight (g)	62.1 ± 0.5	52.4–77.0	32	24
Volume (ml)	61.8 ± 0.5	52.0–75.4	31	18
Shell weight (g)	5.7 ± 0.1	3.8–7.0	46	37
Percentage lipid[c]	5.5 ± 0.1	2.9–7.5	61	38

[a] n = one egg each from 70 separate clutches.

[b] n = 10 complete clutches, 33 eggs.

[c] Lipid reported only for 1977, 1978, and 1979 samples; n = 45 eggs.

size and composition than were females as a whole.

Organochlorine residues and shell thickness.—Chemical analysis of egg contents indicated that DDE and PCBs were the predominant organochlorine pollutants occurring in spoonbill eggs; DDE was present in all of the samples and PCBs were found in 90% of the eggs (Table 6). In general, organochlorine concentrations were low (<2 ppm), though a few of the eggs contained fairly high levels of DDE (up to 15 ppm). Because the residue data were highly skewed, medians rather than means are presented in Table 6 as a better indicator of pollutant levels in eggs. There was no difference ($P > 0.05$, t-test) in DDE concentrations between addled and fresh eggs that would implicate DDE in egg failure. Other organochlorine pesticides detected in spoonbill eggs were dieldrin and chlordane isomers, but these compounds occurred in concentrations less than 0.5 ppm in all instances.

TABLE 6. Organochlorine residues (ppm, wet weight) in Roseate Spoonbill eggs from Nueces Bay, Texas.

Year	n[a]	DDE	PCBs
1977	5	2.8[b] (5)[c] 1.1–15[d]	0.85 (4) ND[e]–1.7
1978	24	2.5 (24) 0.7–7.5	0.83 (18) ND–5.3
1979	16	1.4 (16) 0.4–3.8	0.92 (16) 0.4–3.5
1980	25	1.3 (25) 0.3–5.8	0.47 (25) 0.2–3.1

[a] Number of clutches from which one egg each was analyzed.

[b] Median.

[c] Number of eggs containing detectable residues.

[d] Range.

[e] ND = not detected.

There was no significant difference ($P > 0.05$, analysis of variance) in eggshell thickness of our collections and that of the 1920's (Table 7). Eggshells in 1977–1979 were 5% thinner than those from the pre-DDT era, but the percentage difference was within the range of intraclutch variation (11%) and is not biologically significant. Ohlendorf et al. (1979) reported no significant eggshell thinning in spoonbill eggs collected from Louisiana and Texas between 1947 and 1973. Embryonic development during incubation is believed to decrease shell thickness in some species (Kreitzer 1972), because the developing chick derives the major portion of its calcium from the shell (Simkiss 1967). We found no difference ($P > 0.05$), however, in eggshell thickness of spoonbill eggs in various stages of development (unincubated, 1/4, 2/4, 3/4, and 4/4). Lindvall and Low (1980) found that incubation stage had no measurable effect on eggshell thickness in Western Grebes (*Aechmophorus occidentalis*).

TABLE 7. Eggshell thicknesses (mm) of Roseate Spoonbill eggs from the Texas coast.

Year	n[a]	$\bar{x}$ ± SE	Percentage change
1923–1924[b]	11	0.44 ± 0.01	—
1977	10	0.42 ± 0.01	−5
1978	24	0.42 ± 0.01	−5
1979	16	0.42 ± 0.01	−5
1980	25	0.44 ± 0.01	0

[a] Number of clutches.

[b] Pre-DDT era; measurements from both years were combined.

CONCLUSIONS

Under normal circumstances, the proportion of eggs that produces flying young (nest success) varies widely among avian species and is dependent upon many factors (Ricklefs 1973). Nest success is known to vary from year to year within some species (Maxwell and Kale 1977, Schreiber 1979), and we found this to be true of Roseate Spoonbills. Allen (1942) reported only a 2% nesting success for a Texas spoonbill colony in 1940 because of heavy tick infestation, but in 1941 he estimated that reproduction was excellent in this colony, though no figures on nest success were given. Nest success in our study colony ranged from 36% to 54%, averaging 50%, or 1.5 fledglings per nest for the 3-yr period. Failure of the eggs to hatch and loss of young during the first 2 weeks after hatching appeared to be the greatest limiting factors in spoonbill reproduction. Rodgers (1980) reported that mortality among heron nestlings also was greatest when the chicks were 1–2 weeks of age. In 1980, the year we made frequent visits during the early part of the nesting season, productivity was lowest because of poor hatching success. Human disturbance can adversely affect reproduction, especially in the pre-egg and incubation stages (Schreiber 1979). This was not the case in our study, however; there was no difference in productivity between a portion of the colony visited frequently and one visited only twice. Our visits were most frequent after the chicks had hatched, and this probably lessened our impact, as Schreiber (1979) showed for Brown Pelicans (*Pelecanus occidentalis*).

Reproduction of Roseate Spoonbills in Nueces Bay appeared to be good, based on an overall nesting success of 50%. It is difficult to assess whether or not this figure is adequate to maintain a stable population, not only from a logistics standpoint, as discussed by Schreiber (1979), but also because of a scarcity of comparable reproductive data on this species. Spoonbills are absent from many of the areas in Texas where they formerly bred (Allen 1942), and population numbers probably are far below what they once were. Nevertheless, the present population appears to be holding steady at about 2,500 breeding pairs, according to the Texas Colonial Waterbird Census (Blacklock et al. 1979). For this reason, we believe that nest success is adequate and that the population is in no immediate danger of decline. The population status of this relatively uncommon species should be monitored closely, however, especially because industrial and agricultural development is increasing along the Texas Gulf Coast.

Environmental pollutants (including DDE and other organochlorine compounds) probably had little effect on spoonbill reproduction, though some eggs had fairly high concentrations of DDE. Apparently, spoonbills are less sensitive to DDE than other species, such as the Brown Pelican. Blus et al. (1974) presented convincing evidence that Brown Pelicans suffer nest failure if eggs contain more than about 2.5 ppm (wet weight) DDE; 34% of our spoonbill eggs had DDE levels of this magnitude or higher. Some eggshell thinning was detected, but it was not to the extent (15–20%) known to cause population declines in other avian species (Anderson and Hickey 1972). Levels of other pollutants, such as PCBs, dieldrin, and chlordane, were low in spoonbill eggs and are not suspected of causing reproductive problems.

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HYBRIDIZATION AND BREEDING SUCCESS OF COLLARED AND PIED FLYCATCHERS ON THE ISLAND OF GOTLAND

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ABSTRACT.—Two closely related Old World flycatchers, the Pied Flycatcher (*Ficedula hypoleuca*) and the Collared Flycatcher (*F. albicollis*), are allopatric on most of the European mainland but have overlapping ranges in central and eastern Europe and on the island of Gotland in the Baltic. On Gotland, the Collared Flycatcher is approximately 10 times as abundant as the Pied Flycatcher. The two species hybridize (4% of all matings) at frequencies less than those predicted for random mating (13%). Mixed pairs produce as many offspring as pure Pied Flycatcher pairs and more offspring than Collared Flycatchers. The competence at courtship and/or viability of hybrid offspring, however, is probably reduced, because fewer hybrids breed than would be expected from the proportion of hybrid fledglings.

SPECIES are defined as intrafertile but noninterhybridizing populations, and interspecific hybrids are rarely encountered in most samples of animals under natural conditions. Among birds, interspecific hybrids occur at a frequency of one in about 50,000 (Mayr 1970). We assume that numerous isolating mechanisms owe their existence to selection against interspecific hybridization, which wastes genes. Yet, some bird species pairs remain distinct over much of their common range despite hybridization in certain regions, perhaps especially those regions in which habitats have recently become greatly modified and/or where sympatry is recent (e.g. West 1962, Short 1969, Mayr 1970, Gill 1980). Similarly, largely allopatric species may hybridize in narrow zones of overlap, in which case it is sometimes a matter of taste whether the two are best regarded as species or subspecies. While situations of this kind are commonly described in the literature, quantitative information about the rate of hybridization and the reproductive output of mixed, as opposed to pure, pairs is almost always wanting. Here we report such details for a case of two European allospecies interbreeding in a zone of sympatry.

The species involved are the Pied Flycatcher (*Ficedula hypoleuca*) and the Collared Flycatcher (*F. albicollis*). These Old World flycatchers occur as allospecies (semispecies), with ranges overlapping in central and eastern Europe and on the Baltic islands of Gotland and Öland (Fig. 1). Sympatric populations hybridize to some extent (Löhrl 1955, Alerstam et al. 1978).

Collared and Pied flycatchers are closely related. Both are highly sex-dimorphic in plumage. Males of the two species are easily distinguished from one another, the male Collared Flycatcher differing from the Pied Flycatcher in having a white collar and rump. On the other hand, females are almost indistinguishable in the field by plumage characters. The songs and alarm calls, however, are highly species-specific.

On the island of Gotland, where this study was performed, the total populations of Collared and Pied flycatchers have recently been estimated at 4,000 and 500 pairs, respectively (Gustafsson and Högström in press). The nearest Collared Flycatcher population is found approximately 600 km southeast of Gotland, while the Pied Flycatcher breeds abundantly on the mainland of northern, central, and eastern Europe (see Fig. 1). Collared Flycatchers thus predominate in this peripheral, isolated area within the range of the more northerly Pied Flycatcher.

In the present paper, we attempt to determine whether or not (1) birds mate assortatively and (2) breeding success of interspecific pairs is reduced, as would be expected for true species.

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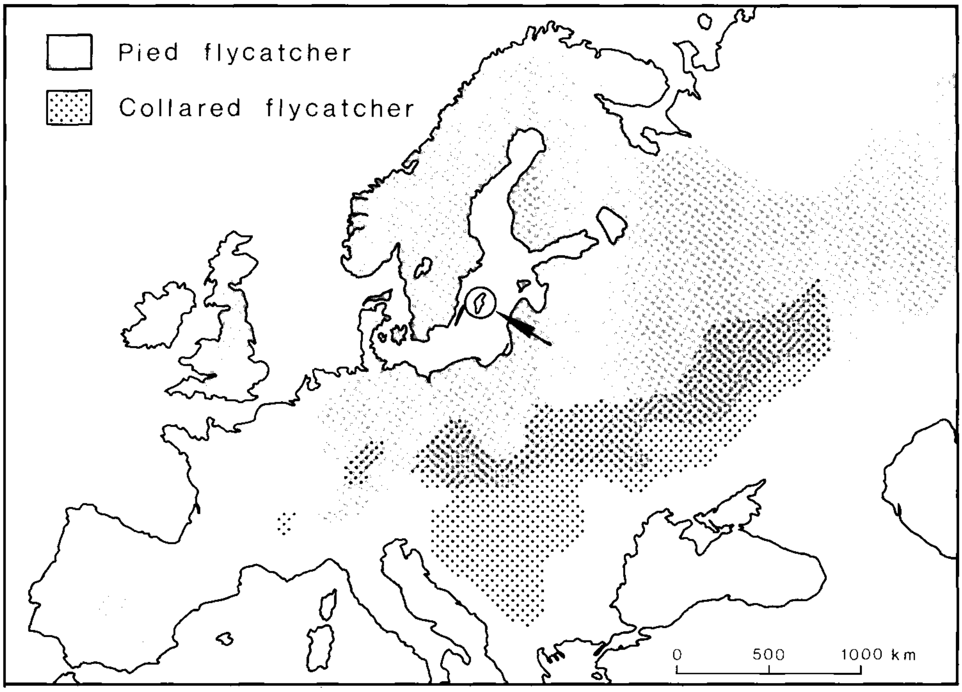

Fig. 1. Breeding ranges of Collared and Pied Flycatchers (based on Alerstam et al. 1978, but modified from Creutz 1970 and Glowacinski 1974). The island of Gotland is encircled.

STUDY AREA AND METHODS

Collared and Pied flycatchers are especially suitable for study because they use tree holes as nest sites. With nest boxes, one is able to control the whole population, because the birds seldom nest in natural cavities when nest boxes are present. We erected a total of 435 nest boxes in two major forest habitats in southern Gotland (57°10′N, 18°20′E). In deciduous woodlands the nest box density was 6/ha and in coniferous forest, 1.5 nest boxes/ha. The deciduous woodlands are dominated by oak (*Quercus robur*) and ash (*Fraxinus excelsior*), with a dense lower layer of hazel (*Corylus avellana*) and hawthorn (*Crataegus* spp.). The coniferous forest is dominated by pine (*Pinus sylvestris*), but birch (*Betula pubescens*) is also common.

The arrival of the flycatcher males and their occupation of territories were monitored by censuses every second day. For each nest we recorded the onset of laying, clutch size, hatching success, and fledgling numbers. We captured and banded all females and almost all males during the nestling period. In some cases we did not succeed in capturing the male, because polygamous males seldom feed the young of their second nests. The species identity of these males was clear, however, from our census records.

Male hybrids can easily be identified from their vague whitish collars. In the hand, hybrid females can be distinguished by the amount of white on their neck feathers (see Svensson 1975). Collared Flycatcher males were classified as old or yearlings on the basis of the color of all primary coverts (Svensson 1975), while Pied Flycatcher males were aged from the innermost primary covert (Alatalo et al. MS).

RESULTS

Hybridization frequency.—The occupancy of nest boxes and the breeding densities of different pair combinations in the two habitats are given in Table 1. The breeding density of flycatchers was 20 times higher in deciduous than in coniferous forest, and many more nest boxes remained unoccupied in the latter habitat. The Collared Flycatcher was almost 30 times as abundant as the Pied Flycatcher in deciduous forest, while in the coniferous area we found only three times as many Collared Flycatchers. The proportion of mixed pairs was much higher in coniferous forest than in deciduous forest (17% and 2.5%, respectively). In addition, we observed four nests in which

TABLE 1. Breeding densities of Pied (PF) and Collared (CF) flycatchers and of mixed pairs in different habitats on the island of Gotland.

Habitat	Size of study areas (ha)	Number of nest boxes	Percentage occupancy by		Density of flycatcher pairs/ha	Density of breeding pairs/ha		
			Fly-catchers	All species		CF × CF	CF × PF	PF × PF
Deciduous woodland	37	243	48.6	75.7	3.19	3.00	0.08	0.11
Coniferous woodland	116	192	9.9	24.0	0.16	0.10	0.03	0.03

one parent bird apparently was a hybrid; these pairs are not included in Table 1.

If the individuals of the two species mated randomly, one would expect 13% of the pairs to be mixed (Table 2). The observed proportion of mixed pairs was 4.4%, however, which deviates significantly ($\chi^2 = 7.66$, $P < 0.01$) from random. Thus, there is an overrepresentation of intraspecific matings, interbreeding occurring only in 36% of the number of cases expected if random mating is assumed. We may expect underrepresentation of mixed pairs, simply because the frequencies of occurrence of the two species are not identical in the two habitats. In each habitat, however, the observed number of mixed pairs was 29% (deciduous: $\chi^2 = 5.11$, $P < 0.05$) and 44% (coniferous: $\chi^2 = 2.51$, $P > 0.10$), lower than expected if random mating is assumed. In 5 of the 7 mixed pairs (including 1 pair outside the main study areas), the male was a Collared Flycatcher and the female a Pied Flycatcher. Moreover, of all Pied Flycatchers, 30% were involved in interspecific matings, whereas the corresponding figure for the Collared Flycatcher was only 2%. Of males involved in interspecific mating, 6 out of 7 (86%) were yearlings. For all intraspecific pairs this proportion was lower (55%), but the difference is not significant (Fisher exact, $P = 0.12$).

Breeding success.—Average clutch size and fledgling numbers of intra- and interspecific pairs are given in Table 3. We have combined the data from the two habitats, because we found no differences in breeding success between habitats. Lundberg et al. (1981) found higher breeding success for the Pied Flycatcher in deciduous than in coniferous habitat, but the difference was small. Laying date affects breeding success much more profoundly than habitat, so comparisons must take the time factor into account. Our data are extensive for the Collared Flycatcher, and we therefore use regression equations for clutch size and fledgling numbers versus the laying date of this species as a reference line. The regression equation for clutch size is: $y = -0.078x + 6.77$ (SD = 0.66, $n = 123$), where x is laying date (day 1 = 20 May). Pied Flycatchers had, on average, 0.71 (SD = 0.84, $n = 7$) more eggs than simultaneously laying Collared Flycatchers (Fig. 2). This difference is significant ($t = 2.70$, $P < 0.01$). The clutch size of mixed pairs was intermediate between that of pure pairs of the two species (0.46 higher than for the Collared Flycatcher, SD = 0.65, $n = 7$, $t = 1.81$, $P < 0.10$).

Hatching success of the flycatchers was high, and no difference emerged among the pair combinations (Table 3). The regression line for fledgling numbers of the Collared Flycatcher decreased more rapidly with time than the line for clutch size (Fig. 3; regression equation for number of fledglings: $y = -0.128x + 6.43$, SD = 1.71, $n = 123$). Early breeders presumably gained from an outbreak of caterpillars, which levelled off in the second half of June.

TABLE 2. Observed and expected mating combinations of flycatchers.

	Pure Collared Fly-catcher pairs	Pure Pied Fly-catcher pairs	Mixed pairs
Number found	123	7	6
Percentage found	90.4	5.1	4.4
Percentage expected	86.3	1.0	12.7

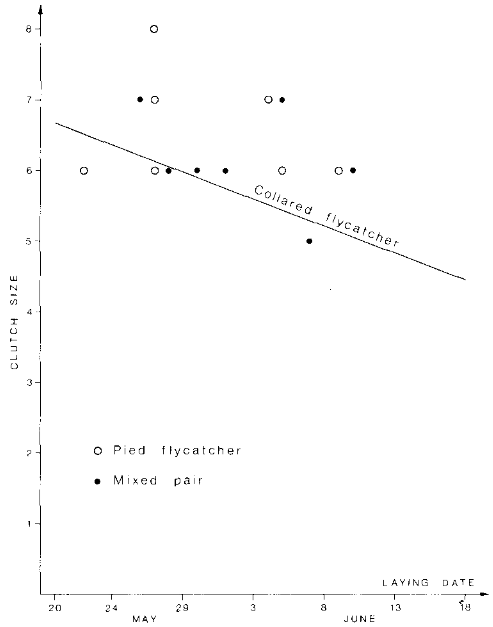

Fig. 2. Clutch size of Pied Flycatchers and of mixed pairs in relation to the regression line for clutch size versus laying date in the Collared Flycatcher.

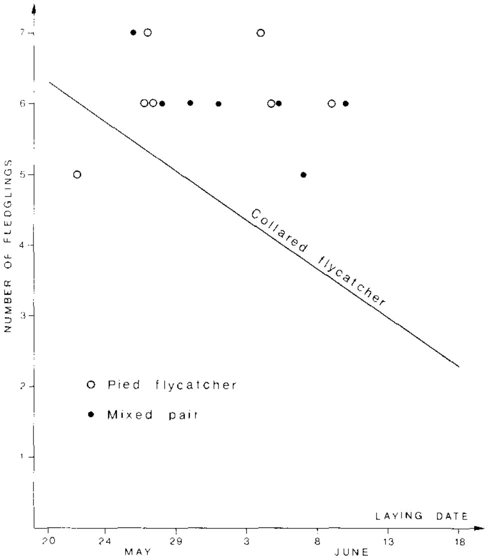

Fig. 3. Number of fledglings of Pied Flycatchers and of mixed pairs in relation to the regression line for fledgling numbers versus laying date in the Collared Flycatcher.

Pied Flycatchers produced, on average, 1.32 (SD = 1.32, $n = 7$) more fledglings than simultaneously breeding Collared Flycatchers (Fig. 3). Unlike clutch-size distributions, the brood-size distributions clearly deviated from normal because of the total failure of some broods. Therefore, t-tests of significance could not be used, and, instead, we calculated for each Collared and Pied flycatcher nest the deviation in fledgling number from that to be expected from the regression line in Fig. 3. In this case, the regression equation is used only to standardize the general decrease in breeding success with season. Between-species differences in terms of such deviations were found to be significant using the Mann-Whitney rank test ($z = 2.17$, $P < 0.05$). Because there is no difference in the mean laying date of the two groups (Table 3), one could compare fledgling numbers discounting the laying date, in which case the difference is still significant (Mann-Whitney; $z = 2.10$, $P < 0.05$). Interspecific pairs were also found to produce significantly more fledglings ($\bar{y} = 1.51$, SD = 0.60, $n = 7$, $z = 2.84$, $P < 0.01$) than simultaneously breeding Collared Flycatchers. No significant difference was found between pure Pied Flycatcher pairs and mixed pairs.

DISCUSSION

In the two flycatcher species, though mixed pairs occur, there is a clear preference for con-

TABLE 3. Breeding data of Pied and Collared flycatchers and of mixed pairs.

Species	n	Mean laying date	Clutch size	SD	Hatched eggs (%)	Fledglings	SD
Collared Flycatcher	123	2 June	5.76	0.81	94.1	4.64	1.90
Pied Flycatcher	7	1 June	6.57	0.79	95.7	6.14	0.69
Mixed pairs	7	3 June	6.14	0.69	100	6.00	0.58

specific mates (Table 2). In two other cases of allospecies hybridization, pairs also mated assortatively [Gill and Murray 1972 (*Vermivora pinus/V. chrysoptera*), Hoffman et al. 1978 (*Larus glaucescens/L. occidentalis*)]. In the latter case, quantitative data were provided. Because only 25% of the *Larus* pairs were pure, the incidence of assortative mating was clearly lower than in this study. In contrast, Ingolfsson (1970) found that *Larus hyperboreus* and *L. argentatus* in Iceland mated randomly.

One would expect marked positive assortative mating if reproductive success of interspecific pairs or of hybrid offspring were low and random mating if hybridization did not reduce reproductive success (Short 1972). Mixed pairs of Collared and Pied flycatchers produced viable offspring. In fact, mixed pairs produced significantly more offspring than Collared Flycatchers (Fig. 2), presumably because the Pied Flycatcher has a larger clutch size than does the Collared Flycatcher (Fig. 2), and most of the mixed pairs involved Pied Flycatcher females.

What happens to the offspring of mixed flycatcher pairs? Hybrids comprised 6.4% of all flycatcher fledglings but only 1.4% of the breeding adults (see also Alerstam et al. 1978). This implies reduced survival or incompetence at courtship. It is not likely that hybrids are less efficient foragers than pure individuals (see Mayr 1970), because the two species are very similar in terms of their foraging habits (Alerstam et al. 1978). On the other hand, the two flycatcher species breeding on Gotland have largely different wintering areas (Moreau 1972), which may cause problems for the hybrids during migration. Hybrid males may be relatively unsuccessful at courtship (Ficken and Ficken 1968, Mayr 1970), because their vocalizations and courtship behavior may differ from the parental species. In fact, the songs of hybrid flycatcher males were clearly different from the songs of the pure species and often included species-specific elements of both the parental species. Also, hybrid female vocalizations differed from those of the parental species.

Offspring from interspecific matings may be fully fertile, may have reduced fertility, or may be sterile (Mayr 1970). For example, captive *Anas platyrhynchos* and *A. acuta* procreated fully fertile hybrids. Hoffman et al. (1978) found high breeding success for hybrids of two *Larus* species under natural conditions. Apparent introgression between several allospecific pairs (for examples, see Anderson 1977) implies that hybrids in many cases are not completely sterile. Brewer (1963; see also Rising 1969) suggested that, in natural populations, hybrids of *Parus atricapillus* and *P. carolinensis* produce less viable offspring. He found a very low fledgling success in six nests in an area of sympatry. Examples of allospecific pairs that produce only F_1 hybrids are given by Anderson (1977). In this study, 2 out of 4 pairs in which hybrids were involved failed to hatch their eggs, while 2 produced young (4 and 6, respectively). In one study plot on the Swedish mainland, (59°50′N, 17°40′E) where the Collared Flycatcher is absent, we found one hybrid male, which was paired with a Pied Flycatcher female. This pair raised four fledglings from six eggs laid. Löhrl (1955) and Vepsäläinen and Järvinen (1977) each found a fertile, breeding, hybrid flycatcher male, but in the latter case the authors mentioned the possibility that the brood could have been adopted by the hybrid male. Thus, in summary, flycatcher hybrids are not fully sterile but apparently do suffer from reduced fertility. Our data are too few to estimate the viability and fertility of hybrids accurately, but, because the two species have retained their specific characters on Gotland so well, introgression can be assumed to be slight.

Alerstam et al. (1978) suggested that hybridization acts as an "agent of competition" between the two flycatcher species on Gotland. Because the Pied Flycatcher is less abundant, a greater proportion of its population will suffer the risk of hybridization (see also Vepsäläinen et al. 1975, Anderson 1977, Vepsäläinen and Järvinen 1977). The considerable rate of hybridization should prevent the Pied Flycatcher from building up its population. The hypothesis is based on the assumption that hybrids are practically sterile. Mixed pairs have high reproductive success, but their hybrid offspring seem to be at a reproductive disadvantage. Our data thus support the hypothesis of Alerstam et al. (1978) in that hybridization may help prevent the Pied Flycatcher from becoming established on Gotland. Conversely, hybridization may limit the ability of the Collared Flycatcher to colonize the north and east European mainland, because the likelihood of hybridization will be very high for a few immigrants (Vepsäläinen et al. 1975). An isolated island like Gotland would be easier to colonize than the mainland, if the Pied Flycatcher were established in Scandinavia before the Collared Flycatcher.

Alerstam et al. (1978) proposed that the small Pied Flycatcher population on Gotland probably is maintained by immigration from the surrounding mainland. We have examined this possibility with the following simple model. We assumed a constant population level of 4,000 Collared Flycatcher pairs and 500 Pied Flycatcher pairs (Gustafsson and Högström in press), a hybridization frequency equivalent to that found in the present study, a 50% adult survival rate to the next year (unpubl. data; see also Anderson 1977), and the same number of offspring per pair of each species surviving to the next breeding season. Then, each year, 73 pairs (=15% of the total population) of Pied Flycatchers have to immigrate to Gotland to compensate for the hybridization losses (if hybridization leads to total reproductive failure). On the other hand, Pied Flycatchers had 32% more fledglings than did the Collared Flycatchers (Table 3). If this difference were maintained until the next breeding, an immigration rate of only 16 Pied Flycatcher pairs per year would be sufficient to retain a stable situation. Because huge numbers of Pied Flycatchers are captured and banded on Gotland during spring migration (Rosvall 1979), an immigration of this modest magnitude may easily be achieved.

The situation is complicated, however, by the fact that the Collared Flycatcher is socially dominant over the Pied Flycatcher (Löhrl 1955). Studies on the Swedish mainland showed that the Pied Flycatcher clearly prefers deciduous forest (Lundberg et al. 1981), but the Collared Flycatcher seems to be able to monopolize the favorable deciduous habitats on Gotland and to relegate the Pied Flycatcher to suboptimal habitats (Table 1). Even if there were no hybridization, we believe that the Collared Flycatcher would survive in its isolated northerly refuge. On the other hand, hybridization may be the prime factor preventing the Collared Flycatcher from establishing a population on the surrounding mainland. One can only speculate about the origin of the present stable distribution of the two species in Scandinavia, but the isolated position of Gotland and the occurrence of hybridization may well be of importance.

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(continued on p. 315)

NESTING SUCCESS OF DICKCISSELS (*SPIZA AMERICANA*) IN PREFERRED AND LESS PREFERRED HABITATS

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ABSTRACT.—Habitat selection in the Dickcissel (*Spiza americana*) was evaluated by a comparison of over 500 nest histories from the preferred oldfield and the less preferred prairie communities in Kansas. Females are equally successful in either habitat, and their productivity is not adversely affected by their being mated to polygynous males. Thus, these two habitats are similarly suitable for females, and females are distributed simply according to the availability of adequate nesting environments and not in any density-dependent manner or in response to density cues. No differences exist in survival rates of nests associated with individual males or in the males' individual productivities between prairies and oldfields when monogamous and bigamous males are compared. The oldfield habitat is more suitable for males, however, because the potential for sequestering more nesting sites is greater in this more heterogeneous habitat. This permits higher levels of polygyny, which increases the productivity of individual males, even though densities of birds in oldfields are greater.
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GRASSLANDS and variously aged oldfields are the two major habitats selected by Dickcissels (*Spiza americana*) for establishment of territories by males and nests by females. The density of males is higher in oldfields than in prairies, and the frequency of polygyny and the average number of females per male is also greater in oldfields (Zimmerman 1971). The greater suitability of preferred oldfields over other habitats appears to be a function of the vegetation, which is more heterogeneous and taller in oldfields, with greater coverage by forbs. The density of males in a particular habitat and the number of females per male in this polygynous species are significantly and positively related to the amount of vegetation present there (Zimmerman 1971). I do not know which attribute of the vegetation structure particularly enhances the attractiveness of oldfield habitats. It could be food. Even though female Dickcissels regularly forage beyond the boundaries of the territory of their mate (Zimmerman 1966), Wittenberger (1980) has suggested several reasons why the proximity of high-quality food resources to the nest still may be crucial. The vegetation probably does not protect the nest from loss to predators (Wittenberger 1976), but the importance of vegetation for nest sites may be through the improvement of the microclimate surrounding the nest and the critical impact of this mitigation on the growth of the young (Blankespoor 1970). Pleszczynska (1978) also has demonstrated the importance of nest-site microclimate for the Lark Bunting (*Calamospiza melanocorys*), the short-grass plains counterpart of the Dickcissel.

Using the predictions based on the models developed by Fretwell and Lucas (1969), which differentiate between the three notions relating territoriality to population regulation (i.e. Huxley 1934, Kluyver and Tinbergen 1953, Lack 1964), one may infer that oldfield habitats are more suitable, even though densities are higher there, because females prefer oldfield males to prairie males. Male Dickcissels thus illustrate the "ideal dominance" distribution (Fretwell and Calver 1969). K. L. Petersen (MS) has shown that the temporal sequence of utilization of different habitats by male Dickcissels follows the pattern expected from the ideal dominance model. Early in the season, when male densities in oldfields are low, no birds settle in grasslands, but, as densities increase in the more preferred oldfields, Dickcissels invade upland prairies, peaking in density a week or so after the oldfield populations have reached maximum numbers but never attaining the high densities characteristic of oldfields.

The ultimate measure of habitat suitability, of course, is the productivity of birds. As Fretwell and Lucas write (1969: 33), "If a species has an ideal territorial (dominance) distribution, then the success rate in habitats with higher densities of residents will be higher." Whitham (1980) has pointed out that the Fretwell-Lucas hypotheses have been largely untested because of the difficulty of measuring fitness in habitats of known quality. The purpose of this paper is to use the Fretwell-Lucas hypotheses to identify the habitat distribution systems of male and female Dickcissels through a comparison of nest survival rates and the production of young from over 500 nests in oldfields and prairies, habitats clearly differing in quality.

METHODS

Nest data were gathered from 1965 through 1979 from populations on the Ft. Riley Military Reservation and the Konza Prairie Research Natural Area in Riley and Geary counties, Kansas, deep within the center of the area with highest breeding densities of this species in North America (Robbins and Van Velzen 1969). Except for a few populations for which nests were visited every 3 or 4 days, most data were obtained by checking nest contents once a week. The fates of nests in which young were expected to fledge during the intervening period and that were found empty at the next visit were easily determined by the behavior of the females. A female with fledged young gives agonistic displays and continues to feed the young in the vicinity of the nest for several days before moving further away with the brood. A female whose nest has suffered predation immediately disappears. In some populations birds were color-banded, so that male territories and the densities and mating patterns of males and females could be determined weekly. In these situations, then, it also was possible for me to relate the success of individual nests to the specific male presumed to be genetically involved, by observing either copulation or the companionate behavior of the pair during the early days of nesting. Although "stolen" copulations among marked birds have not been observed, they may occur from time to time. For the purpose of this analysis, however, I have assumed that the observed mate is probably the biological parent, so that these nests could then be used to measure the success and productivity of males as well as of females according to the polygynous status of the male.

Johnson (1979) has validated the efficacy of the Mayfield (1961, 1975) nest-exposure method of estimating nesting success and has effectively answered the critics of this procedure. Furthermore, he has provided a formula by which confidence limits for survival rates may be calculated, thus permitting unbiased comparisons between the probabilities of nest survival in different populations. Accordingly, daily nest survival rates were determined for the separate stages of the nesting cycle in oldfields and prairies. Additionally, daily survival rates of nests were computed on a per-male basis for males with differing levels of polygyny by summing all days of nest exposure for all nests of males with just 1 nest on their territories (including the monogamous males involved with several single nests sequentially during a single season) and of polygynous males with 2–6 nests active on their territories. This number of nests is not exactly the same as the male's harem size, because not all nests for a given male were simultaneous. Rather, this value is used as a measure of the suitability of a male's territory, as reflected by the use of his area for nesting by different females. This procedure compensates for differences in reproductive effort among males with different levels of polygyny and isolates the effect that differences in the numbers of nests might have on the assessment of males' nesting successes. In all analyses, samples for males with 5 and 6 nests were pooled to make the total sample size similar to that of the other nest categories.

While recognizing Mayfield's (1961) caveat regarding the biases inherent in determining the numbers of fledglings produced per nest found, I have calculated this value for nests in both habitats as a measure of the average productivity per female and have also converted this value into an average per male by summing the production for all nests present in a male's territory.

RESULTS

Nesting phenology.—The week of initiation of nest construction was known or, in most cases, estimated for 397 oldfield nests and 130 prairie nests. Nesting begins earlier in oldfields than in prairies and spans a longer season (Fig. 1). The peak week of nest starts, however, is the same for both habitats (15–21 June), but 50% of all prairie nest starts occur in the 3-week period from 15 June to 5 July, while 50% of all nest starts in the oldfield span a broader period, 8 June–5 July. The difference in the variance of these two populations is significant ($F = 1.65$, $df_1 = 396$, $df_2 = 129$, $P < 0.01$). These data are consistent with the population data gathered by Petersen (MS) and parallel the difference in settlement dates of Indigo Buntings (*Passerina cyanea*), another polygynous species, in high-density and low-density habitats (Carey and Nolan 1979).

Clutch size.—A total of 149 nonparasitized nests was known to have complete clutches. The 15 prairie nests in this total contained from 3 to 5 eggs with a mean of 4.0 (SE = 0.14), and the 134 oldfield nests contained from 2 to 6 eggs with a mean of 4.0 (SE = 0.07).

Although it is not possible to determine with certainty the number of Dickcissel eggs actually laid in nests parasitized by the Brown-headed Cowbird (*Molothrus ater*), due to host egg removal by the cowbirds, there is no significant difference between habitats in the number of Dickcissel eggs present in parasitized nests at the beginning of incubation. For 193 oldfield nests the mean was 2.4 eggs (SE = 0.09), and for 96 prairie nests the mean was 2.5 eggs (SE = 0.12).

There is, however, a significant difference in the mean number of cowbird eggs per nest in parasitized oldfield nests (2.3, $n = 201$, SE = 0.10) compared to those in the prairie, (2.9, $n = 96$, SE = 0.16) (Student's $t = 3.28$, df = 295, $P < 0.01$). The higher intensity of cowbird parasitism in the prairie (Elliott 1978) results in the total clutch of Dickcissel and cowbird eggs in prairie nests ($\bar{x} = 5.2$, SE = 0.16, $n = 111$) being significantly different from the total clutch in oldfield nests ($\bar{x} = 4.5$, SE = 0.08, $n = 330$) (Student's $t = 4.34$, df = 439, $P < 0.01$). The larger combined clutch size of prairie nests, however, does not in itself decrease the chances for survival of the young; within the same habitat there is no significant relationship between clutch size and survival rate (Zimmerman MS).

Female success.—Female Dickcissels are single-brooded. For all the nest histories of marked individuals, no two nests that successfully fledged young were produced by the same female in the same year. The length of nest life (average 26 days) and the postfledging care of the brood (about 2 weeks), when compared with the period during which reproduction is energetically feasible (Zimmerman 1965), precludes second successful broods. Indeed, I have never observed a successful female initiate a second attempt.

Females do renest after the failure of an earlier attempt. This sometimes occurs within the territory of the same male (17% of the time) or with another male in the same local population (10% of the time), but most frequently the female disappears and is not seen again. These unsuccessful females may seek out other fields of the same habitat type, or perhaps they select different habitats. Thus, population data from preferred oldfield study plots show a continued increase in female density until mid-July, as females enter the habitat after presumed failures elsewhere or for some reason have delayed initiation of nesting. For the purpose of this analysis, therefore, I have considered the probability of nest survival and the productivity per nest attempted to approximate the success of the average individual female in each habitat.

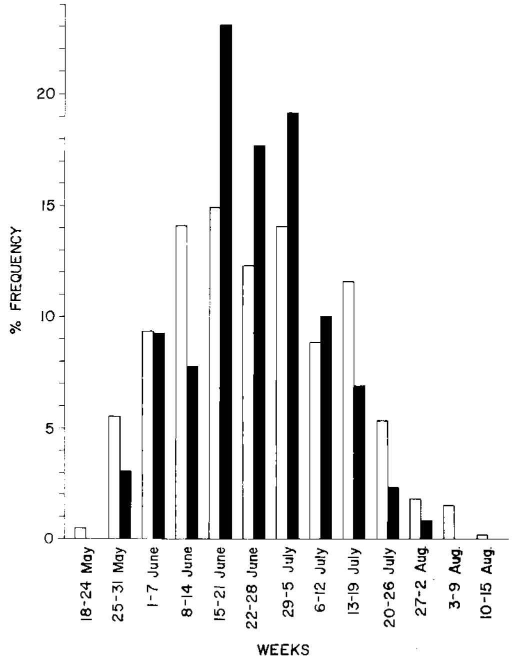

Fig. 1. Percentage frequency distribution of oldfield nest starts (open bars) and prairie nest starts (shaded bars) with the weeks of the nesting season.

The daily survival rates computed for 137 prairie nests and 413 oldfield nests are presented for each phase of the nesting cycle (Table 1). The daily survival rates in each habitat were not significantly different among phases of nesting. The overall probability for survival can be calculated by raising the probability of each phase to the power equal to the number of days in that phase and then multiplying these separate probabilities together. Thus, oldfield nests have a 14.3% chance of being successful, while prairie nests have a similar value of 15.2%. Although female densities are higher in oldfields than in prairies (Zimmerman 1971), the estimated survival rate of nests of individual females in each of these two habitats is the same.

Even though the survival rates are similar, during the nest-building and egg-laying periods the values for prairie nests are lower than those for oldfield nests, while during the in-

TABLE 1. Daily survival rates of nests.

	Building		Egg-laying		Incubation		Brooding	
	Oldfield	Prairie	Oldfield	Prairie	Oldfield	Prairie	Oldfield	Prairie
Mean days in phase	2	2	3	3	12[a]	12[a]	9[b]	9[b]
Total days of nest exposure	185	23	405	81	2,117	624	1,056	534
Number of nests lost	13	2	49	15	164	34	53	25
Daily survival rate	0.930	0.913	0.879	0.815	0.922	0.946	0.952	0.955
±95% C.L.	0.04	0.12	0.03	0.09	0.01	0.02	0.01	0.02

[a] Incubation starts with day the last egg is laid.
[b] Includes the day of hatching.

cubation and brooding phases they are higher. This is explained by the greater impact of cowbird parasitism in the prairie, which leads to nest abandonment during construction and egg laying, and the higher incidence of predation in the oldfield (Zimmerman MS).

Production of Dickcissels per nest attempted is similar in oldfield ($\bar{x}$ = 0.72, n = 396, SE = 0.068) and prairie ($\bar{x}$ = 0.87, n = 115, SE = 0.122). There is, however, a significant difference in the total numbers of Dickcissels and cowbirds fledged per nest attempted between oldfield ($\bar{x}$ = 0.94, n = 396, SE = 0.081) and prairie ($\bar{x}$ = 1.42, n = 125, SE = 0.171) (Student's t = 2.774, df = 519, $P < 0.01$). This result is related to the significantly larger clutch size in prairie nests due to the heavier cowbird parasitism.

For a subset of these nests, mating relationships were known. It is therefore possible to compare the mean production of fledglings per nest in both habitats according to different levels of territory suitability as indicated by the numbers of mates attracted by the males (Table 2). No significant association occurs between the number of mates a male attracts, that is, the quality of his territory, and the average productivity of females involved, nor is there a significant difference between habitats in the productivity of females mated to males with equivalent numbers of mates. It should be noted that the number of mates used for this comparison is not strictly equivalent to the harem size of the males, but, as in other polygynous species (Holm 1973, Weatherhead and Robertson 1977, Carey and Nolan 1979), the success of the female is not lessened by her being mated to a polygynous male.

Male success.—Some polygynous males were involved with as many as five simultaneous mates in oldfields, while two were the maximum in the prairie (Table 3). The survival rates of a male's nests were analyzed according to the total numbers of females he attracted (Table 4). Again, this ranking is not exactly the same as the harem size. The probability of survival of a male's nests, if he has just one or two, is the same regardless of habitat. Furthermore, no difference exists between the daily survival rates of nests according to the number of nests per male in either habitat, nor does a significant association occur between the number of nests per male and the daily survival rates for the nests of these males.

TABLE 2. Production of fledglings/nest attempted ($\bar{x}$ ± SE) according to the number of females attracted to the territory.

	Oldfield			Prairie		
Number of mates	Number of nests	Dickcissel	Dickcissel + Cowbird	Number of nests	Dickcissel	Dickcissel + Cowbird
1	83	0.84 ± 0.16	1.01 ± 0.18	22	1.18 ± 0.31	1.73 ± 0.45
2	52	0.92 ± 0.22	1.31 ± 0.26	20	1.10 ± 0.38	1.45 ± 0.46
3	75	0.88 ± 0.16	1.08 ± 0.19			
4	72	0.50 ± 0.14	0.67 ± 0.18			
5 and 6	46	0.63 ± 0.21	0.72 ± 0.22			

TABLE 3. Numbers of males according to maximum number of simultaneous mates/male (percentage within each habitat).

Number of females	Prairie	Oldfield
One	23 (74.2)	75 (51.0)
Two	8 (25.8)	43 (29.2)
Three	0	24 (16.3)
Four	0	4 (2.7)
Five	0	1 (0.7)

The mean number of Dickcissel young/male, or the total number of Dickcissel and cowbird young/male, is not significantly different when males with one or two nests are compared between habitats, nor do any significant differences exist among prairie males in the numbers of Dickcissels or Dickcissels plus cowbirds produced. In the oldfield, on the other hand, there are significant differences between the mean numbers of young produced by males with just one nest and males with two nests, both for Dickcissels fledged (Student's $t = 3.194$, df = 94, $P < 0.05$) and for Dickcissel and cowbird young together (Student's $t = 3.194$, df = 94, $P < 0.01$). Males with 3 or more nests also produce significantly more young than males with 1 nest, but the numbers of young produced by males with 2, 3, 4, 5, and 6 nests are not significantly different from each other. Furthermore, there is a significant positive association between the number of nests of a male and the numbers of both Dickcissels and total young fledged/male in the oldfield habitat (Spearman $r = 0.9$, $n = 5$, $P < 0.05$).

DISCUSSION

The female Dickcissel most certainly has a set of criteria that she uses to select an appropriate nesting location. As they arrive during spring migration and presumably are attracted by the singing and other displays of territorial males, females discover suitable nest sites and begin to build. I do not know what involvement the male has in nest-site selection, but I do know that the behavioral interaction of the male with the female during this critical period is intense (Schartz and Zimmerman 1971). It is also not known whether the female chooses a territory on the basis of male phenotype (Weatherhead and Robertson 1979), and thus incidentally obtains access to a suitable nest site, or selects the nesting situation directly using criteria of microhabitat quality (Searcy 1979). Of course, it could be both, as Weatherhead and Robertson suggest. Yet, if females were choosing solely on the basis of the quality of the male rather than that of the nesting habitat, some females would certainly end up with unsuitable nest sites as harem size increased, assuming a limited number of nest sites, and there would be a decline in nesting success. This does not happen, however (Tables 2 and 4).

Because there is no significant difference between survival rates of oldfield and prairie nests (Table 1) nor any difference between

TABLE 4. Daily nest survival rates (±95% C.L.) and production of fledglings/male ($\bar{x} \pm SE$) according to the number of females attracted to the territory.

	Number of different females/male				
	1	2	3	4	5 and 6
Oldfield					
Number of males	70	26	25	18	8
Survival rate	0.930 ± 0.02	0.940 ± 0.02	0.944 ± 0.02	0.913 ± 0.02	0.912 ± 0.03
Dickcissel young	1.00 ± 0.19	1.85 ± 0.45	1.64 ± 0.50	2.00 ± 0.48	3.62 ± 1.13
Dickcissel and Cowbird young	1.20 ± 0.21	2.62 ± 0.47	3.24 ± 0.57	2.67 ± 0.62	4.12 ± 1.12
Prairie					
Number of males	22	9			
Survival rate	0.954 ± 0.03	0.931 ± 0.04			
Dickcissel young	1.18 ± 0.31	2.44 ± 0.82			
Dickcissel and Cowbird young	1.73 ± 0.45	3.22 ± 1.23			

these two habitats in the number of Dickcissel young produced by each female, the two habitats have equal suitability for the female. Any individual nesting location in the prairie is just as good as a nesting site in an oldfield. Females fill up the habitat or, more precisely, occupy adequate nest sites according to their availability. The distribution of females is not determined by the territory boundaries of the males nor in any density-dependent manner by the numbers of females themselves (for example, female-female aggression has never been observed).

An important corollary to this conclusion is that females mated to polygynous males are not at a disadvantage (Tables 2 and 4). Such a relationship is to be expected from the threshold model for the evolution of polygyny (Verner 1964, Verner and Willson 1966, Orians 1969).

If females spread themselves across the landscape simply as a function of the distribution of suitable nesting sites, it is important for the male to include as many suitable sites as possible in his territory. Prairie males do just as well at this as oldfield males when they are monogamous or bigamous (Table 4). The enhanced suitability of the oldfield habitat for males, however, lies in its providing for higher orders of polygyny, which augment male productivity (Table 4) even though male density is greater. These data support the ideal dominance model for the distribution of male Dickcissels (Fretwell and Lucas 1969).

Thus, three different patterns interact in the distribution of Dickcissels across the available habitat space. The heterogeneity of the vegetative substrate results in an uneven distribution of potentially suitable nesting situations within habitats as well as between habitats (Zimmerman 1971). The males' territories are then superimposed upon the habitats, but suitable nesting sites are not equitably apportioned among the males. Not all the territories in the same habitat are equal in quality, and territories in different habitats also differ in quality (Zimmerman 1971). A male that controls a high-quality territory with multiple nesting situations will attract more mates and gain greater fitness. The male's size, the signalling value of his plumage, the aggressiveness of his behavior, his experience, and other attributes have been suggested as possible factors that might explain observed differences in the abilities of polygynous Red-winged Blackbird (*Agelaius phoeniceus*) males to obtain numerous mates (Searcy 1979, Yasukawa 1979), but supporting data are weak or lacking. Similar factors may assist male Dickcissels in obtaining good territories, and they are being tested (Finck MS).

Females, on the other hand, simply distribute themselves as a function of the availability of nesting situations, with nests built in any habitat and in any territory being equally suitable to the female as long as the site is adequate for nesting. She loses nothing by choosing a nest site within the territory of a male that is already mated. She only loses if she chooses to mate with a male that is defending an area lacking a suitable nesting environment. The regular occurrence of bachelor males (Zimmerman 1966) suggests that females do not make this mistake very often.

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A STUDY OF FASTING IN TREE SPARROWS (*SPIZELLA ARBOREA*) AND DARK-EYED JUNCOS (*JUNCO HYEMALIS*): ECOLOGICAL IMPLICATIONS

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Abstract.—Despite similarities in winter distribution, habitat selection, and food choice, Dark-eyed Juncos (*Junco hyemalis*) and Tree Sparrows (*Spizella arborea*) differ in the extent to which they store fat during winter, with juncos accumulating greater stores. Anticipating that Tree Sparrows might have some means of conserving energy during fasting and thus suffer no disadvantage when weather prevents feeding, we compared the species for weight loss, body temperature, and locomotor activity during fasting and noted relative fasting endurance. Because both species exhibit geographic variation in sex ratio during winter, we also made sexual comparisons, anticipating that males would be able to fast longer than females. The species responded similarly to fasting by (a) lowering body temperature, especially at night, and (b) becoming hyperactive, progressively more so as fasting time increased. Tree Sparrows did not exhibit these responses to a greater degree (although they became hyperactive sooner) and were not able to fast as long as juncos. No sexual differences in fasting ability were observed. Because the species-specific difference in tendency toward fat accumulation cannot be attributed to differences in energy expenditure while fasting, at least in the laboratory, other explanations are considered. *Received 22 June 1981, accepted 21 September 1981.*

Tree Sparrows and Dark-eyed Juncos that winter in the northern half of the eastern United States have similar ground-feeding habits and overlapping diets and sometimes forage together in mixed flocks (West 1967, Bent 1968, Willson 1971, Pulliam and Enders 1971, Coulter pers. comm.). Their ability to meet energy requirements is surely severely tested during winter at times when cold is intense, nights are long, and snow covers food for prolonged periods or storms prevent feeding. Like many other species that winter in the north-temperate zone, juncos and Tree Sparrows increase deposits of body fat in winter (Helms et al. 1967, Helms and Smythe 1969), a response that is commonly accepted as an adaptation to provide energy during forced fasting (e.g. King 1972, Ketterson and King 1977). In both species, the sexes tend to separate by latitude in winter, with females settling in milder climates (Ketterson and Nolan 1976, 1979, unpubl. data), a behavior that could be related in part to sexual differences in the ability to withstand severe weather. Yet despite the similarities of these two small sparrows and despite the fact that populations wintering at the same location encounter identical weather, the two species differ in the reserves of energy stored as fat. Juncos have been reported to store fat in an amount that is 12–17% of their mean wet winter weight (Helms et al. 1967); by comparison, the figure for Tree Sparrows is only 5–12% (Helms and Smythe 1969). This difference led us to test experimentally the prediction that Tree Sparrows either (1) cannot endure fasting for as long as juncos, or (2) compensate for their reduced energy stores by conserving energy in ways not used by juncos.

Fasting endurance is determined by the ratio of energy stored to the rate of energy utilized, and, because per-gram metabolic rate is negatively correlated with body size, fasting endurance is theoretically affected by body size (Calder 1974). Thus, larger species, or larger size classes within a species, might be expected to be able to fast longer than smaller ones if the individuals being compared store fat in similar proportion to their body weight. Because juncos are somewhat larger than Tree Sparrows, they might therefore be expected to show greater fasting endurance, even in the absence of their disproportionate fat stores already mentioned. Further, both species are

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sexually dimorphic in size, and as no significant sexual differences in fat stores (as a percentage of body weight) have been observed (Helms et al. 1967, Helms and Smythe 1969), fasting endurance in both species might also be greater in the larger sex, the male.

Decreases in body temperature are for birds a common means of saving energy during fasting (Baldwin and Kendeigh 1932, Biebach 1977, deGraw and Snelling pers. comm., Ketterson and King 1977). Hyperactivity, presumably the result of hunger, is also typical of fasted, caged birds and in the field would lead to more active searching for food (Wagner 1937, Eyster 1954, Merkel 1966, deGraw and Snelling pers. comm., Ketterson and King 1977). The extent to which hyperactivity incurs an energy cost is not known, because heat generated by exercise may fully or partially substitute for thermoregulatory costs, depending on the level of activity, air temperature, and perhaps nutritional state (Ketterson and King 1977, Paladino 1979). These considerations suggested that Tree Sparrows could employ marked body temperature lability to save energy during fasting but might or might not conserve energy by diminished locomotor activity. In any case, a difference between the two species in locomotor response to fasting would call for further investigation.

In the work reported here, we first determined that juncos and Tree Sparrows at Bloomington, Indiana conformed to the general pattern of greater fat storage by juncos and then investigated the following questions:

1. Did fasting endurance of the two species differ?
2. Regardless of the answer to 1, did fasting Tree Sparrows develop hyperactivity to a greater or lesser extent than fasting juncos or exhibit greater or less lability in body temperature?
3. Recalling the sexual difference in distribution in each species in winter, did fasting affect the sexes differently in either or both species?

These questions were investigated using newly caught birds (as in Kendeigh 1945, Biebach 1977) rather than captive birds (as in Ivacic and Labisky 1973, deGraw and Snelling pers. comm., Ketterson and King 1977). Evidence that captive birds differ from wild birds in fat deposition and cold acclimatization (Kendeigh 1949, Hart 1962, King and Farner 1966, Helms and Smythe 1969) suggests that studies of fasting in birds newly taken from the wild may yield more reliable results.

We note here (and discuss below) that the ability to fast is only one factor that might affect winter survival and that carrying excess fat may have its costs (Helms and Smythe 1969). Evidence that winter fat levels may sometimes be regulated below maximum capacity is provided by reports that some bird species are fatter preceding migration than during midwinter (Linsdale and Sumner 1934, Baumgartner 1938, Wolfson 1945, Odum 1949, King et al. 1963, King 1972) and by the observation that juncos of equal body dimensions are fatter in winter at northern than at southern latitudes (Ketterson and Nolan unpubl. data). Thus, a final objective of this paper is to consider circumstances that might select against maximal fat storage.

METHODS

Ten Tree Sparrows and 18 juncos were confined in a windless room at 8–10°C on a 10L:14D photoperiod and deprived of food until death seemed imminent (as defined below). Body temperature (T_b) of some birds and weights of all were taken every 4 h [or sometimes 8 h, because recordings (hereafter RT, recording time) at 0330 were irregular], while locomotor activity was monitored continuously. Controls were birds treated similarly except that they were given unlimited access to a mixture of turkey starter mash, millet, ground eggs, beef, and carrots. All birds were provided with water and were caged individually so that none could see any other bird.

Some controls did not eat and lost weight at the same rate as experimentals, a response to captivity that we have occasionally observed in various other seed-eating fringillids. To eliminate the confounding effects of data from such individuals, we have omitted their weights, T_b's, and activity from all calculations. Controls, therefore, included only individuals whose percentage weight loss, if any, was at least 20% less than that of the experimental bird of the same species that exhibited the smallest percentage weight loss. All controls, so defined, gained weight at least once between successive RTs, indicating that they were eating. Seven Tree Sparrows and 14 juncos satisfied the criteria for inclusion as controls, and 3 Tree Sparrows and 8 juncos did not. We now think that had the birds not been visually isolated, this loss of data could have been avoided.

Six experiments were conducted between 13 January and 15 February 1981. On the day each was to begin, we captured as many juncos and Tree Sparrows as possible (extremes 4 and 16) between 1450

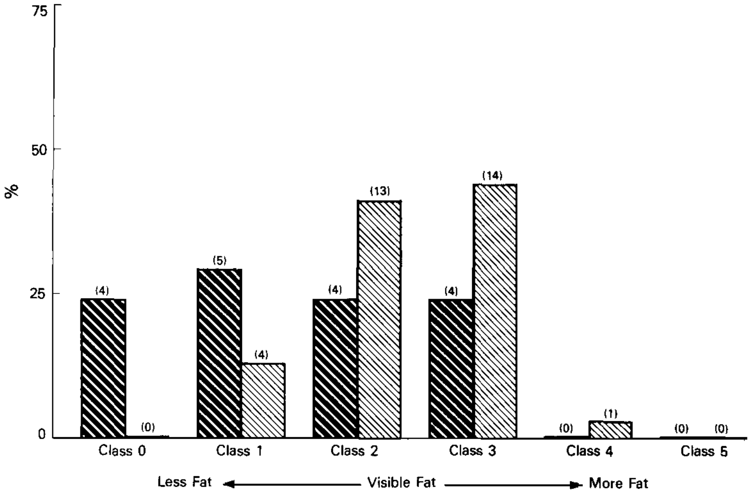

Fig. 1. Percentage of juncos and Tree Sparrows according to fat class at capture. Sample sizes as indicated in parentheses include both the experimental subjects and those controls that satisifed criteria for inclusion (see text). Light bars = Dark-eyed Juncos, dark bars = Tree Sparrows.

and 1830. These we weighed immediately in the field (Pesola spring balance, 50-g capacity, nearest 0.1 g) and transported to the laboratory, where we measured the flattened wing and classed for fat according to a modified version of the scale described by Helms and Drury (1960). Juncos we sexed at the time of capture using the criteria of Ketterson and Nolan (1976), whereas Tree Sparrows were sexed by laparotomy after the completion of all experiments. Experiments were conducted too late in the year to permit us to age subjects. Birds destined to be fasted or fed were assigned to these classes randomly.

Each bird was weighed again 4 h after capture when the gut may be assumed to have been empty (Kontongiannis 1967), and this weight we designate as "initial weight." Birds were transferred to the cold room between 2045 and 2215. Each was placed in a small cage (22 cm × 26 cm × 28 cm) equipped with a single perch attached to a microswitch; each hop on the perch was recorded on an Esterline-Angus event recorder. In order to minimize the effects of disturbance, T_b measurements were made on only a subset of subjects (maximum, 10) in each experiment; subjects were taken from the cold room one at a time in a prescribed order and a Schultheis quick-responding thermometer was inserted into the cloaca for 30 s (nearest 0.1°C). In the first experiment, an experimental bird's T_b was measured first, then a control bird's, then an experimental's; in the second experiment, a control bird was measured first.

TABLE 1. Comparisons of fasted Dark-eyed Juncos and Tree Sparrows in a 10°C cold room, sexes pooled.

Measurement	Juncos (n = 18)[a]	Tree Sparrows (n = 10)[a]	t	P
Wing length (mm)[b]	79.7 ± 0.72	75.8 ± 0.84	3.34	<0.01
Initial weight (g)[c]	20.78 ± 0.39	18.27 ± 0.32	4.36	<0.001
Final weight (g)[d]	15.63 ± 0.22	14.74 ± 0.25	2.54	<0.05
Weight loss (g)[e]	5.16 ± 0.24	3.44 ± 0.19	3.52	<0.01
Percentage weight loss[f]	24.5 ± 1.25	17.6 ± 0.90	3.18	<0.01
Rate of loss (g/h)[g]	0.120 ± 0.004	0.120 ± 0.008	0.07	n.s.
Fasting endurance (h)[h]	43.19 ± 2.79	29.51 ± 2.02	3.38	<0.01

[a] Mean ± 1 SE.
[b] Flattened wing.
[c] Four h after capture (i.e. gut contents voided).
[d] At time bird believed to be within 4 h of death.
[e] (Initial weight − final weight).
[f] (Weight loss/initial weight) × 100.
[g] (Weight loss/h endured).
[h] Number of hours elapsed between time initial weight taken (i.e. 4 h after capture) and termination of experiment (see text).

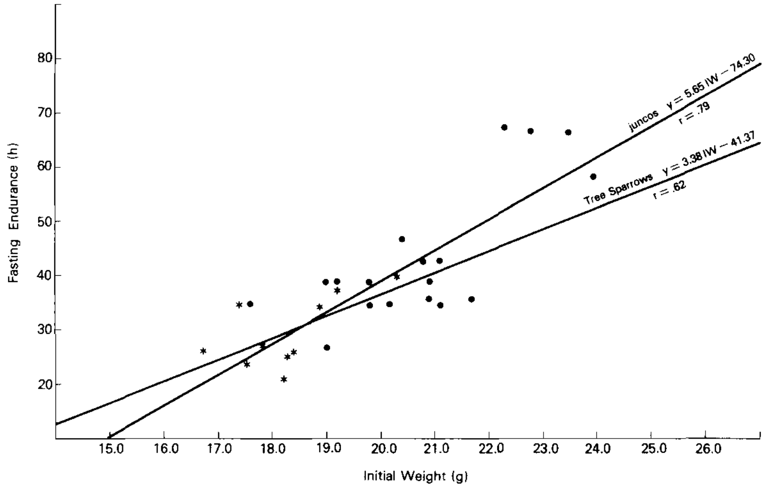

Fig. 2. Relationship between initial weight and fasting endurance for Tree Sparrows (*) and juncos (●). In regression equations, Y stands for fasting endurance and IW for initial weight (see text).

The alternation of experimentals and controls and the order in which the first subject was selected was continued for the remainder of the experiments. When T_b measurement was completed, body weights of all individuals in the experiment were taken as before and recorded.

For experimental birds, the experiment was terminated at the RT when death appeared imminent using the standards of Ketterson and King (1977). For controls, the experiment was terminated when the last experimental was removed. Ketterson and King (1977) report that death could be expected within 4 h in White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) that erected the feathers of the head, breast, and back, were very lethargic, held the eyes partly closed, and sometimes refused food when presented. Fasted juncos and Tree Sparrows behaved similarly and also tucked the head into the scapular feathers when severely stressed. Tree Sparrows showed all signs of stress to a greater degree than juncos. The application of the foregoing subjective standard to determine when death was approaching introduces some error into our results, but we believe that it is similar for the two species. Equal efforts were made to restore experimental birds at the end of experiments (they were warmed and supplied with food, including hand feeding of glucose and water), but two juncos (11%) and four (40%) Tree Sparrows died within 24 h after removal from their cages. Fasting endurance was calculated as the number of hours elapsed between the time the bird's gut could be assumed empty (4 h after capture) and the time that death was judged imminent.

To summarize activity data, we selected blocks of time 1.5 h in length from each 4-h interval between RTs, specifically, the 1.5-h block beginning 2.5 h before the next RT. Blocks are assumed to have been representative of the 4-h intervals. Because caged birds develop idiosyncratic patterns of movement that may only occasionally include landing on the perch, within each 1.5-h block we counted only the number of 30-s intervals in which the individual activated its perch. Thus, activity scores could range between 180 and 0. Occasionally a perch would stick or a pen would fail to write; consequently, the number of individuals comprising a sample sometimes varied among RTs.

RESULTS

Fat class.—As predicted from the findings of Helms and Drury (1960), Helms et al. (1967), and Helms and Smythe (1969), juncos showed more visible fat when captured than did Tree Sparrows (Fig. 1). The actual values of the fat classes reported here are lower than those of Helms and Drury (1960), but we believe that this is due to a difference in application of the 0–5 scale and not to a difference in fat. In any case, the difference between the species is comparable.

Fasting endurance and weight loss.—The mean duration of fasting of the experimental juncos was 43 h and the extremes 34 h and 67 h; mean weight loss was 25% of initial weight and the extremes 19% and 36% (Table 1). In contrast, mean fasting endurance of the Tree Sparrows was 30 h and the extremes 21 h and 40 h; mean

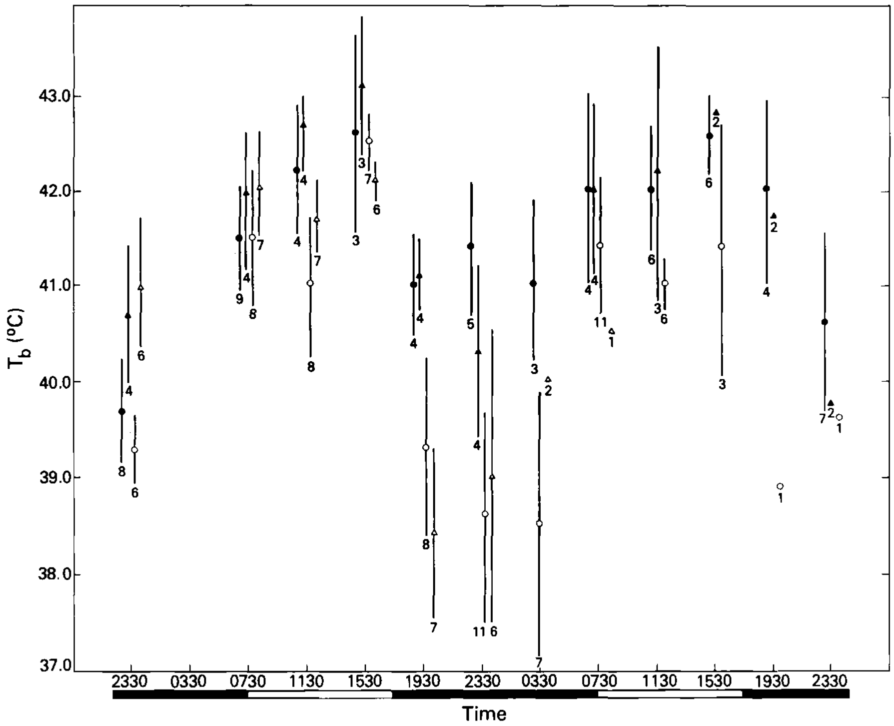

Fig. 3. Mean body temperature of fasted (○) and fed (●) juncos and fasted (△) and fed (▲) Tree Sparrows kept in a 10°C cold room. Vertical lines represent ±2 SE. Sample size is indicated below the line. Open horizontal bars indicate daylight hours; closed bars indicate dark hours.

weight loss was 18% and the extremes 14% and 24% (Table 1).

The mean rate of weight loss per hour was identical in the two species. In each species, initial weight significantly predicted fasting endurance: in the juncos, fasting endurance = 5.65 (initial weight) − 74.30, $r^2 = 0.62$; in Tree Sparrows, fasting endurance = 3.38 (initial weight) − 41.37, $r^2 = 0.39$ (Fig. 2). The difference in the slope of the lines suggests that in juncos a given weight change reflects a greater increase or decrease in fasting endurance than in Tree Sparrows, but the difference was not significant (in juncos, $s_b = 1.11$, in Tree Sparrows, $s_b = 1.73$ where s_b is the standard error of the regression coefficient).

Body temperature.—Control juncos and Tree Sparrows had very similar T_b's. Differences were recorded at 2330 on nights 1 and 2 (Fig. 3, Table 2), but the differences were inconsistent. In one case, the mean for Tree Sparrows was greater; in the other, the mean for juncos was greater.

When the effects of fasting first became apparent (after 0730 on the first day of fasting), fasted birds of both species tended to drop their temperatures below those of controls, and the differences were greater at night (Fig. 3, Table 2, experimental vs. control body temperatures differed significantly in both species except juncos, 1530 day 1, 0730 and 1530 day 2; Tree Sparrows 2330 night 2, one-tailed Mann-Whitney *U*-tests).

Fasted birds showed no species-specific difference in the extent to which T_b dropped: T_b's differed significantly only at 1530 on day 1 when the mean for fasted Tree Sparrows was below that of fasted juncos. (For some unknown reason, juncos had lower body temperatures than Tree Sparrows at 2330 night 1, before the effects of prolonged fasting could have set in.)

The extreme T_b's recorded in fasted juncos were 35.2°C and 43.4°C; the comparable figures for control juncos were 38.9°C and 43.7°C. In fasted Tree Sparrows, extreme T_b's were 35.6°C

TABLE 2. Body temperature comparisons of fasted (experimental) and fed (control) Dark-eyed Juncos and Tree Sparrows.[a,b]

	Within species		Between species	
Time	Experimental vs. control juncos Medians/n_e, n_c (U,P)	Experimental vs. control Tree Sparrows Medians/n_e, n_c (U,P)	Control juncos vs. control Tree Sparrows Medians/n_j, n_s (U,P)	Experimental juncos vs. experimental Tree Sparrows Medians/n_j, n_s (U,P)
2330	39.4, 39.6/6, 8 (15, n.s.)	41.0, 40.6/6, 4 (9, n.s.)	39.6, 40.6/8, 4 (3, $P < 0.014$)	39.4, 41.0/6, 6 (0, $P < 0.001$)
0730	41.4, 41.4/8, 9 (36, n.s.)	42.2, 42.2/7, 4 (13.5, n.s.)	41.4, 42.2/9, 4 (14, n.s.)	41.1, 42.2/8, 7 (18.5, n.s.)
1130	41.1, 42.2/8, 4 (4.5, $P < 0.030$)	41.7, 42.7/7, 4 (1, $P < 0.006$)	42.2, 42.7/4, 4 (5, n.s.)	41.1, 41.7/8, 7 (15, n.s.)
1530	42.4, 42.4/7, 3 (10, n.s.)	42.0, 43.0/6, 3 (0.5, $P < 0.018$)	42.4, 43.0/3, 3 (2, n.s.)	42.4, 42.0/7, 6 (7, $P < 0.026$)
1930	39.3, 40.8/8, 4 (4.5, $P < 0.030$)	38.5, 41.4/7, 4 (0, $P < 0.003$)	40.8, 41.4/4, 4 (6.5, n.s.)	39.3, 38.5/8, 7 (17, n.s.)
2330	38.8, 41.4/11, 5 (4.5, $P < 0.010$)	39.4, 40.2/6, 4 (6, n.s.)	41.4, 40.2/5, 4 (2, $P < 0.032$)	38.8, 39.4/11, 6 (29, n.s.)
0330	38.6, 40.5/7, 3 (2, $P < 0.033$)	—	—	38.6, 40.0/7, 2 (2, n.s.)
0730	42.0, 42.2/11, 4 (16, n.s.)	—	42.2, 41.8/4, 4 (8, n.s.)	—
1130	41.0, 42.3/6, 6 (5.5, $P < 0.026$)	—	42.3, 42.1/6, 3 (8.5, n.s.)	—
1530	40.9, 42.6/3, 6 (4.5, n.s.)	—	42.6, 42.8/6, 2 (5, n.s.)	—
1930	—	—	42.2, 41.7/4, 2 (4, n.s.)	—

[a] n_e = sample size of experimental birds of indicated species; n_c = sample size of controls; n_j = sample size of juncos of indicated category (i.e. experimentals or controls); n_s = sample size of Tree Sparrows.

[b] U values are the Mann-Whitney statistic, P values are one-tailed probabilities from Siegal (1956).

and 42.8°C, and in control Tree Sparrows, 38.1°C and 43.8°C.

Activity.—We had expected nocturnal activity in fasted individuals, because previous workers had reported it [Ketterson and King 1977, C. W. Helms pers. obs. of White-throated Sparrows (*Zonotrichia albicollis*)], but virtually none was observed. During the day the fasted birds of both species were more active than controls (Fig. 4 and 5, Mann-Whitney U-tests). When the activity of experimentals and controls is compared for each 1.5-h block, fasting Tree Sparrows became significantly more active than their controls beginning at 1300 on the first full day of fasting. By comparison, fasted juncos first became significantly more active than their controls at 1300 on the second full day of fasting. For both species, once the difference between experimentals and controls appeared, it remained until the final measurements were made and even tended to increase progressively.

Sexual differences.—In Table 3 there is a comparison for each species of experimental birds according to sex. Males of both species had longer wings than females, male juncos had significantly heavier initial weights and final weights, and male and female Tree Sparrows did not differ significantly in weight either at the outset or the termination of experiments. In neither species did the sexes differ significantly in absolute weight loss, percentage weight loss, or rate of weight loss. Furthermore, and contrary to expectation (Ketterson

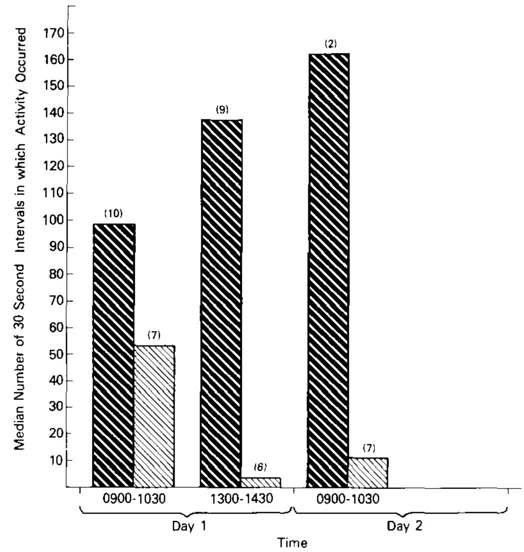

Fig. 4. Daytime activity of fasted and fed Tree Sparrows in a 10°C cold room. Dark bars = fasted Tree Sparrows, light bars = fed Tree Sparrows. Sample size is indicated in parentheses.

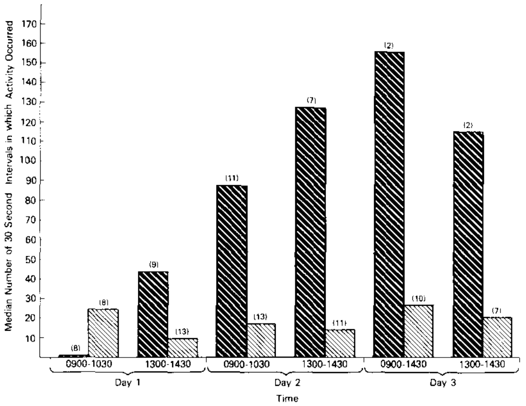

Fig. 5. Daytime activity of fasted and fed Dark-eyed Juncos in a 10°C cold room. Dark bars = fasted juncos, light bars = fed juncos. Sample size is indicated in parentheses.

and Nolan 1976, 1978; Ketterson and King 1977), no significant sexual difference in fasting endurance was detected.

Discussion

The finding that the average experimental junco could fast for about 43 h at an ambient temperature a few degrees above freezing and that the average Tree Sparrow could last about 30 h is consistent with the determination by Ketterson and King (1977) that the mean fasting endurance of another sparrow, the White-crowned Sparrow, is about 38.6 h. White-crowned Sparrows typically carry fat reserves (as a percentage of body weight) larger than those of Tree Sparrows but smaller than those of juncos (King and Farner 1966, Helms et al. 1967, Helms and Smythe 1969).

Because our experiments began late in the day when fat stores are near their peak in the daily fat cycle, our results suggest that free-living juncos whose food first became unavailable in the late afternoon might be expected to last that night and the following day and night. Tree Sparrows under the same conditions might last that night and the following day. Juncos under conditions comparable to those of the experiment would probably survive if food became available again during or immediately after the second night of fasting, whereas Tree Sparrows, even if they had access to food late in the day of the first day of fasting, would be forced to endure another long night and presumably would die.

We found no evidence that Tree Sparrows reduce metabolic expenditure during fasting to a greater degree than juncos. Unlike Black-capped Chickadees (*Parus atricapillus*), which regulate nocturnal T_b about 10–12°C below diurnal T_b (Chaplin 1974), our Tree Sparrows dropped their T_b by only about 1–2°C, i.e. no more than juncos. Neither was there an activity response that would seem to result in energy saving: Tree Sparrows, like juncos, became hyperactive. Interestingly, the timing of the hyperactivity—later in juncos—implies that it is not triggered by the time since feeding occurred, but rather at some level of remaining energy stores. Although, as indicated above, the activity response shown by a fasted bird does not necessarily imply a concurrent increase in energy expenditure, the Tree Sparrow's early increase of activity cannot be construed as an unusual energy-saving adaptation to permit it to carry lower fat stores than juncos.

The reasons for the difference in fat levels of Tree Sparrows and juncos remain obscure, but four possibilities may deserve attention. The first two relate to the relative need for stored energy reserves in the two species.

First, under natural conditions, the species may differ in the actual cost of thermoregulation due to differences in microhabitats selected for roosting or a tendency toward nocturnal huddling, i.e. differences that would not be apparent when housed singly under laboratory conditions. We find no evidence in the literature that juncos or Tree Sparrows huddle at night, however, as do some species (Kendeigh 1945, Frazer and Nolan 1959, King and Farner 1966, King 1972, Haftorn 1972, Chaplin 1974), and both Kendeigh (1945) and Bent (1968) describe roosting behavior that seems much the same for juncos and Tree Sparrows. Kendeigh reports that "the slate-colored junco and tree sparrow normally spend the night in dense ground vegetation or in thickets." We observed both juncos and Tree Sparrows in winter roosts in a large outdoor aviary; the behavior and locations chosen by the two seemed about the same, and no huddling was observed in either species. As a second consideration regarding the relative need for stored energy in the two species, the feeding behavior of Tree Sparrows may be sufficiently flexible to permit them to forage and find food in situations in which juncos must fast. For example, Tree Sparrows may turn more readily than juncos from ground-feeding to foraging from plants emerging from snow cover. Reports of the feeding habits of the two species (Knappen 1934, Baumgartner 1937, Bent 1968, Coulter pers. comm.) do not reveal whether Tree Sparrows have such an advantage, but the subject warrants investigation.

The third and fourth possibilities that may account for the difference in stored fat are related to the idea that fat storage may impose costs and that the magnitude of the cost may vary as a function of the habitats selected by a species or as a function of its body size. That is, it may be disadvantageous to be too fat (Helms and Smythe 1969). Thus, if the foraging locations of Tree Sparrows make them more vulnerable than juncos to avian predators and if an increase in fat stores lowers the probability of escape, perhaps through lowered agility, Tree Sparrows might sacrifice a measure of fasting endurance for the sake of increased agility. According to Helms and Drury (1960), Tree Sparrows do feed in more open areas than juncos, and we too have found that juncos stay nearer to cover than do Tree Sparrows. Studies on the relative agility of the two species at various levels of fat deposition are currently un-

TABLE 3. Characteristics of male and female fasted Dark-eyed Juncos and Tree Sparrows in a 10°C cold room.

Measurement	Juncos[a]				Tree Sparrows[a]			
	♂♂ (n = 13)	♀♀ (n = 5)	t	P	♂♂ (n = 3)	♀♀ (n = 7)	t	P
Wing length (mm)[b]	81.1 ± 0.62	76.0 ± 0.55	4.72	<0.001	79.3 ± 0.88	74.3 ± 0.36	6.51	<0.001
Initial weight (g)[c]	21.40 ± 0.39	19.20 ± 0.47	3.10	<0.01	19.00 ± 0.67	18.00 ± 0.33	1.50	n.s.
Final weight (g)[d]	16.02 ± 0.22	14.64 ± 0.21	3.62	<0.01	15.30 ± 0.31	14.50 ± 0.29	1.62	n.s.
Weight loss (g)[e]	5.37 ± 0.44	4.60 ± 0.43	1.00	n.s.	3.37 ± 0.54	3.47 ± 0.19	0.24	n.s.
Percentage weight loss[f]	24.8 ± 1.62	23.8 ± 1.76	0.35	n.s.	17.6 ± 2.20	19.3 ± 0.94	0.84	n.s.
Rate of loss (g/h)[g]	0.120 ± 0.003	0.120 ± 0.012	0.06	n.s.	0.120 ± 0.015	0.119 ± 0.011	0.06	n.s.
Fasting endurance (h)[h]	44.93 ± 3.70	38.66 ± 2.23	1.01	n.s.	28.72 ± 5.60	29.85 ± 2.05	0.24	n.s.

[a] Mean ± 1 SE.
[b] Flattened wing.
[c] Four h after capture (i.e. gut contents voided).
[d] At time bird believed to be within 4 h of death.
[e] (Initial weight − final weight).
[f] (Weight loss/initial weight) × 100.
[g] (Weight loss/h endured).
[h] Number of hours elapsed between time initial weight taken (i.e. 4 h after capture) and termination of experiment (see text).

derway. Fourth, the cost of locomotion may increase with level of fat deposition, and the extent of the increase could be greater to the smaller-bodied Tree Sparrow. Paladino and King (1979) have estimated the cost of transport in terrestrial locomotion (cm^3 O_2 $(g - km)^{-1}$) as equal to 3.2 (grams body mass)$^{-0.26}$. Thus, if an individual's body weight were to increase from 15 to 20 g, per-gram cost of transport would decrease from 1.56 to 1.45, but per-bird cost would increase from 23.7 to 29.4 cm^3 O_2 km^{-1}, i.e. 19.2%. A comparable increase in weight from 21 to 26 g would alter the per-bird cost from 30.5 to 35.7 cm^3 O_2 km^{-1} or 14.6%. Use of a similar equation for the cost of transport described by Fedak and Seeherman (1979) gives comparable results (18.7%, 14.3%). These differences are obviously small and may have little biological significance. The relative cost, however, of hopping on a treadmill to lean and fat individuals of both species is currently under investigation.

The absence of the expected sexual difference in fasting endurance remains unexplained. Two points regarding our methods, however, make us uncertain about the generality of our data on this point. First, samples were small, and we note that the larger sexual difference among juncos was in the expected direction. Second, the initial weight of subjects differed between trials, presumably because the weather in the days preceding capture efforts was, as is usual for Indiana, quite variable. When prior weather was cold and snowy (trials 1 and 4), subjects tended to be fatter than when prior temperatures were mild (trials 2, 3, 5, and 6). This fact did not affect our species comparisons, because equal proportions of juncos and Tree Sparrows began each trial. Had more females than males been the subjects of trials 1 and 4, while more males than females had been the subjects of the other trials, the failure to observe a sexual difference could have been attributed to chance. Within species, however, both sexes were represented in each trial, so there was no obvious bias. Still, the effect of the differences in initial weight among trials was to increase the variance in fasting endurance, making statistical significance less likely. For this reason we feel the question of a sexual difference in fasting endurance deserves further attention, but note that a causal relationship between fasting endurance and geographic variation in winter sex ratio must be viewed with increased skepticism (Myers 1981). In any case, it seems worth emphasizing that, because fat stores for a species differ from time to time and place to place, it is not possible to characterize just one value for a species' fasting endurance.

Although the reasons for the different levels of winter fat in Tree Sparrows and Dark-eyed Juncos have not been clarified, what is clear is that the two species respond to fasting in the same manner and that Tree Sparrows, when deprived of food, become stressed sooner than juncos unless they resort to some energy-saving behavior that we have not yet been able to detect.

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NOTES ON THE MYOLOGY OF THE PELVIC LIMB IN KIWI (*APTERYX*) AND IN OTHER BIRDS

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Abstract.—Anatomical variants of the musculature of the pelvic limb in *Apteryx*, based on a review of the published literature, are considered from the aspect of (1) errors in descriptive myology, (2) probable misidentification or misrepresentation of muscles, and (3) variations in a given muscle set that have not been thoroughly examined in terms of a form-function complex. A more accurate interpretation of these relationships is suggested as a basis for further studies of the pelvic limb myology in birds. *Received 2 March 1981, accepted 30 June 1981.*

The first account of the somatic musculature of any species of kiwi (*Apteryx australis, A. haastii, A. owenii*) was apparently based on a paper read by Richard Owen on 22 February 1842 and published as a "descriptive portion of this communication" in the *Proceedings of the Zoological Society of London* of the same year (pp. 22–41). The principal muscles described included the extensive, striated Musculi subcutanei, the trunk musculature, shoulder muscles, and the muscles of the pelvic limb. Later some of this descriptive material was incorporated into a longer paper with the addition of plates of illustrations (1849). The latter was essentially reprinted in Owen's "Memoirs" (1879).

In the 35 yr subsequent to these memoirs, there were at least five additional papers that considered the somatic musculature of *Apteryx* based, at least in part, upon independent dissections. These include, in chronological order, the well-known papers of Garrod on the thigh muscles (1873, see Fig. 6, *A. owenii*) and on the deep plantar tendons in birds [1875, see Fig. 2, *A. "mantelli"* (=*australis*)], the general anatomy and embryology paper of Parker (1891) as well as that of Beddard (1899), selected comments by Pycraft (1900), and finally the comprehensive study of Mitchell (1913) on the peroneal musculature in birds ("three examples" of *Apteryx*, p. 1043). The most recent paper on the subject is that of McGowan (1979) on the musculature of the pelvic limb in *A. australis* based on a dissection of two specimens.

In many of the preceding studies, the somatic musculature of kiwis is often described with reference to that of the "ratites" or "palaeognathous" birds (see, e.g. Garrod and Mitchell). The pelvic musculature of the latter is described by Gadow (1880) and Pycraft (1900). More recently, Hudson et al. (1972) describe the appendicular musculature of tinamous, a group that some consider to be allied with ratites. (There is some indication that the latter investigators also dissected at least one specimen of *Apteryx*; see p. 248.)

Although McGowan completed his recent study in an attempt to resolve certain "shortcomings" in descriptive myology (what he later equates with "lapsi calami," p. 64), I propose to review and discuss at least three of his descriptions of morphological variation in the pelvic musculature of *A. australis* that seem to differ significantly from anatomical variants described in other specimens of *A. australis*, in other species of kiwi, and in at least some other avian groups. I will also show that certain components of the pelvic musculature are apparently not described by McGowan, or anyone else, in any specimens of the kiwi.

One of these anatomical variants, namely M. iliotrochantericus medius, is a constituent of the expanded Garrod muscle formula (symbol C; see Hudson 1937: 12). I suggest that this muscle is incompletely described in many avian groups and is, therefore, not sufficiently well-known in terms of morphological relationships to justify its use in terms of conclusions regarding phylogenetic affiliation. I will show that two other anatomical variants, in the peroneal musculature and in the deep digital flexor muscles, are most probably described both inaccurately and incompletely by Owen and McGowan and, in the latter study, are the basis for erroneous statements regarding possible phylogenetic affinities among *Apteryx,* "ratites," and other birds. Finally, I will suggest that a restudy of at least one muscle set, M. caudo-iliofemoralis, may serve as a test of the evolution of functional modalities in a muscle complex and as a related test of recent theories of paleognath monophyly (Bock 1963, Cracraft 1974).

My review of these anatomical variants, from the aspect of descriptive morphology, is based on my interpretation of descriptive data and illustrations in all previously cited references regarding *Apteryx,* my own previous dissections of specimens exemplifying numerous avian groups (Hudson et al. 1966, 1969, with Hudson's unpublished notes on Falconiformes as well as Charadrii; Vanden Berge 1970, 1975, 1976), and my own participation in the substantial review of avian musculature incorporated in the first attempt to formulate a standardized nomenclature (see Myologia in "Nomina Anatomica Avium," Baumel et al. 1979).

Mm. iliotrochantericus caudalis (="posterior"), cranialis (="anterior"), medius. Synonymy: Owen (1842, 1849, 1879), glutaeus medius, minimus (cranialis and medius included); Beddard (1899), glutaeus secundus, tertius, quartus.

M. iliotrochantericus caudalis is apparently the largest of these three muscles in *Apteryx,* as in most other birds (but see George and Berger 1966: 390); the insertion on Trochanter femoris (Baumel 1979a) is subtended by a Bursa synovialis (Vanden Berge 1979) in *A. australis* (Owen 1842: 34) and most likely in other birds as well in view of the probable functional role of this muscle (Cracraft 1971).

According to McGowan (1979: 51), M. iliotrochantericus cranialis is absent in one of two specimens of *A. australis;* medius is presumably present in both. This variant seems to be rather unusual among birds generally. M. iliotrochantericus medius is more frequently described as "absent" in birds, if it is not independently developed with respect to M. iliotrochantericus cranialis, and, instead, is characterized by some continuity of the respective tendons of insertion if not the actual aponeurotic sheath of the contractile tissue itself. This is the basis upon which Beddard (1899: 395) described the variation of the two muscles in *A. australis* and *A. haastii,* and this is also the basis upon which Hudson (1937: 12) suggested that the variants of medius be recognized by formula letter "C." Owen initially stated that "[medius] is peculiar to *Apteryx,* and the preceding portion [i.e. cranialis] is absent in most birds" (1842: 34), but later stated that "one of them (i.e. either cranialis or medius) is absent in most birds" (1879: 55). Intraspecific variation in relative development of certain muscles does occur among birds (see, e.g. Raikow 1975, Raikow et al. 1979) and may have occurred then in McGowan's two specimens of *A. australis.*

I suggest that the passage of a neurovascular bundle (N. coxalis cranialis, Breazile and Yasuda 1979) between the respective proximal attachments of the cranialis and medius muscles (see George and Berger 1966, Klemm 1969, Vanden Berge 1970) is a principal morphological criterion for assessing the anatomical status of both muscles in any avian specimen. In my experience, this criterion seems to be uniformly applicable among birds and is more "predictable" than suggested variations in continuity of the tendons of insertion in terms of "presence" or "absence" of either muscle. Until such time as this interrelationship of a neurovascular bundle to proximal attachments of the two muscles is more fully described, the addition of M. iliotrochantericus medius as a component of the Garrod leg-muscle formula will be of limited significance in terms of designating any degree of phylogenetic affinity among birds (see Table IX in George and Berger 1966).

One other component of the expanded Garrod leg-muscle formula, namely "V," the Vinculum tendinum flexorum, which binds the tendon of M. flexor perforans et perforatus digiti III to that of M. flexor perforatus digiti III as these two tendons traverse the foot, is of uncertain status in the kiwi: present, according to Beddard (1899: 398); absent, according to McGowan (1979: 62); no relationship described in any of Owen's three papers. Furthermore, M. flexor hallucis brevis and M. adductor digiti II are two muscles that *no one* describes in *any* specimen of kiwi, at least to my knowledge. Both muscles are described in some tinamous (Hudson et al. 1972); M. adductor digiti II is apparently present in *Rhea* and *Casuarius* but absent in *Struthio* (Gadow 1880).

Mm. fibularis (peroneus) longus and brevis. Synonymy: longus is equivalent to "superficialis" and brevis to "profundus," as described by some investigators (see, e.g., Mitchell 1913).

According to McGowan (p. 72), the tendon of insertion of M. peroneus longus does *not* form a conjoined tendon with that of M. flexor perforatus digiti III in his specimens of *A. australis,* although this statement appears to contradict his description of both muscles (pp. 60–61 and pp. 64–65) as well as his illustrations (Figs. 17, 18, 22, and 23). McGowan also states that this anatomical variant represents a morphological distinction between ratites and carinates and that this distinction is supported by the original description in Gadow (1880).

The five principal morphological characteristics of M. peroneus longus in terms of a general avian pattern (as exemplified in *Chauna chavaria,* Anhimidae) include (1) a large, fleshy, superficial belly on the craniolateral aspect of the crus; (2) a deep attachment along the shaft of the fibula; (3) a tendinous connection (aponeurosis) to the Cartilago tibialis (see Baumel 1979a); (4) a tendon that traverses a bony sulcus on the lateral aspect of the proximal end of the tarsometatarsus; and (5) the formation of a conjoined tendon where the tendon of insertion unites with that of M. flexor perforatus digiti III on the plantar aspect of the foot. In the kiwi and in ratites, these five characteristics differ from *Chauna* only in "minor detail," according to Mitchell (1913). Gadow (1880: 45) describes the conjoined tendon in *Struthio, Rhea,* and *Casuarius* as follows: "Diese Sehne [M. peroneus longus]—sich mit der Sehne des M. flexor perforatus digiti medii (M. flexor perforatus digiti III) verbindet und daher zur Zehenbeugung beiträgt." On the basis of these two references, the anatomical variant of M. peroneus longus in *Apteryx* is similar to that in other ratites and similar to that in at least some other avian groups, despite the statements to the contrary as given in McGowan.

Although both Owen (1849: 295–296, Plates 31, 32, and 35, tendon 7; 1879: 59–60, Plate II) and Beddard (1899: 397) describe a conjoined tendon, they either describe a most unusual *intraspecific* morphological variation in *Apteryx australis,* or they inadvertently introduce considerable confusion in use of the term "perforatus" and "perforans" in terms of the associated digital flexor muscle (see Myologia, "Nomina Anatomica Avium," Annot. 121; see also Frewein 1967 and Greenlee et al. 1975 for a discussion of the digital flexor tendons and their tendon sheaths as described for *Gallus*). Confusion in the proper use of the descriptive terms seems to be most probable. For example, Owen's description of the conjoined tendon and his illustrations in the 1849 paper differ from those in the memoirs of 1879. In all of the above papers, however, the *tendon of M. peroneus longus does become conjoined* with a tendon of a digital flexor muscle, most probably that of M. flexor perforatus digiti III, in sharp contrast to McGowan's statement as previously cited.

In contrast to the morphological variation in M. peroneus longus in *Apteryx,* M. peroneus brevis is said to be very much reduced in terms of relative development (Mitchell 1913: 1043) and apparently absent in some specimens (Beddard 1899: 397). Owen, in fact, does not describe a "typical" brevis in any of his three papers.

McGowan describes a short peroneal muscle in his specimens of *A. australis.* In the next section, however, I will attempt to show that "peroneus brevis" as described by McGowan is a synonym for "peroneus medius" in Owen's papers (1849, 1879, but *not* 1842) and that, in both cases, the muscle so described has no morphological relationship to the peroneal musculature described in other birds. In fact, it is probably *not* a component of the peroneal musculature at all.

M. flexor hallucis longus. Synonymy: Owen (1842, 1849, 1879), M. flexor perforans digitorum, tendon 1; McGowan (1979), M. flexor digitorum longus.

M. flexor digitorum longus. Synonymy: Owen (1842), M. flexor perforans digitorum; Owen (1849 and 1879), "Peroneus medius Cuvier, Accessorius flexoris digitorum Vicq d' Azyr"; Beddard (1899), M. flexor profundus; McGowan (1979), M. peroneus brevis.

According to McGowan (p. 65), M. flexor hallucis longus, as a deep digital flexor of the hallux, is *not* present in either specimen of *A. australis* that he dissected, although he states that the muscle is represented by a specific tendon of "flexor digitorum longus" to the hallux. The anatomical relationships of this latter muscle as described in his specimens of *Apteryx* differ very little from those of M. flexor hallucis longus described in other specimens of kiwi

(Beddard 1899). Furthermore, the morphological relationship of the long (deep) flexor of the hallux to the deep flexor of the digits in *A. australis* is illustrated as a definitive example of Type II morphological variant in the original paper on this subject (Garrod 1875: 341, Fig. 2; see also Gadow and Selenka 1891).

If the muscle described by McGowan as "flexor digitorum longus" is, in fact, M. flexor hallucis longus, then either M. flexor digitorum longus is itself absent in the same specimens of kiwi, or the deep digital flexor muscle is likewise misidentified. The latter is almost certainly the case here, based on McGowan's description of the anatomical relationships of "peroneus brevis" with respect to its proximal attachments in the crus, the position of the tendon as it traverses the tibial cartilage, the formation of a conjoined tendon (with M. flexor hallucis longus) in the foot, and a trifurcation into a deep flexor tendon to each of the three toes. M. peroneus brevis has never been so described in any other birds (see Mitchell 1913, Hudson 1937, and numerous other investigators), and the above mentioned morphological characters are those most often associated with M. flexor digitorum longus.

As previously mentioned, Owen does not describe M. peroneus brevis in any of his three papers, nor any other muscle having the expected morphology described for other birds. Furthermore, the anatomical description of "flexor perforans digitorum" (1842: 40–41) is virtually identical to that of "Peroneus medius Cuvier, Accessorius flexoris digitorum Vicq d' Azyr" of the later papers (1849, 1879). In all three papers, Owen states that the tendon of insertion "receives a strong accessorial tendon *from the muscle which bends the innermost toe,* and finally divides into three strong perforating tendons" (emphasis mine). Gadow (1880: 51) gives an interesting footnote to what he describes as the "outer head of flexor profundus." In that footnote he quotes directly from Owen's paper of 1849 and clearly states that Owen's use of "Peroneus medius Cuvier, Accessorius flexoris digitorum Vicq d' Azyr" as a synonym for M. flexor digitorum longus in *Apteryx* was erroneous and that Cuvier, at least, was describing M. peroneus longus! I am not able to confirm this reference to the work of Cuvier, however.

In view of the apparent discrepancies between the morphological relationships of the peroneal musculature and deep digital flexor muscles as described in *Apteryx* by Owen, Beddard, Mitchell, and McGowan, and the same relationships in ratites and other birds, McGowan's statement (p. 72) that "the fusion of the tendons of insertion of the Mm. peroneus brevis and flexor digitorum longus is not unique to *Apteryx* but is a condition which is shared with other ratites," is not substantiated.

The preceding review of the status of the peroneal musculature, and the deep digital flexor muscles, suggests that neither of these muscle sets is predictive of phylogenetic relationships between *Apteryx* and ratites, or between ratites (collectively) and other birds. They do *not* constitute a "distinction between ratites and carinates," as suggested by McGowan (1979: 71–72).

M. caudo-iliofemoralis: M. caudofemoralis, M. iliofemoralis. Synonymy: Owen (1842, 1849, 1879), M. adductor brevis femoris, M. adductor longus; Garrod (1873), Beddard (1899), femoro-caudal and accessory femoro-caudal (including also "superficial femoro-caudal"?); McGowan (1979), M. piriformis, pars caudofemoralis, pars iliofemoralis.

Both axial and pelvic components of this muscle complex are present in *Apteryx*. The axial component, M. caudofemoralis, is differentiated from the pelvic component even though it is "slender, straplike, of only moderate size" (McGowan 1979: 53). This muscle is also described as the "femoro-caudal" and is illustrated in *A. owenii* (Garrod 1873, Fig. 6). Beddard (1899), however, indicates that there is no clear separation between the two muscle components in other specimens of kiwi.

M. caudofemoralis is clearly differentiated in most tinamous (except *Eudromia*, Hudson et al. 1972), but much less so in ratites. The caudofemoralis is very weakly differentiated in *Struthio* (Gadow 1880) and *Casuarius* (Gadow 1880, Garrod 1873, Pycraft 1900) and absent in *Rhea* and *Dromaius* (Garrod 1873, Pycraft 1900). Other variants of this muscle in carinate birds are well known in the literature (George and Berger 1966, Table IX, symbol A).

Of particular interest, however, is the apparent hypertrophic development of the pelvic constituent, M. iliofemoralis, in *Apteryx* (*A. owenii*, Garrod 1873, Fig. 6; *A. australis*, McGowan 1979, Figs. 10 and 11) as well as in some ratites (*Casuarius*, Gadow 1880, Plate III, Fig.

1; Pycraft 1900, Fig. 6), and in tinamous (Hudson et al. 1972, Fig. 10). In all of these specimens, as illustrated, the proximal "fixed" attachment of M. iliofemoralis is "perforated" by peripheral branches of *Plexus sacralis* and accompanying vessels, principally *Arteria ischiadica* (Baumel 1979b; *not* "femoral vessels" as labelled in McGowan's Figs. 9–11), as this neurovascular bundle emerges through Foramen ilioischiadica to enter the postacetabular region of the thigh. The distal (functional) attachment of this muscle in these avian groups includes an extensive linear attachment on the shaft of the femur, apparently separate from (but contiguous with) the femoral aponeurosis of M. caudofemoralis (see, e.g. McGowan, pp. 52–53).

If the M. caudo-iliofemoralis complex in birds is derived from the coccygeofemorales muscle system in reptiles, as suggested by Romer (1927), then M. caudofemoralis may be assumed to be the "primitive" component and to be of common occurrence among birds. Also, the principal morphological and functional relationships of this axial component would be correlated with the musculature of the tail (see Fisher 1957, Owre 1967, Baumel 1971, Cracraft 1971), rather than the pelvic limb.

M. iliofemoralis would then represent a secondarily derived, appendicular component (see Romer 1927) whereby the muscle set gained a stationary attachment to the postacetabular ilium (and ischium, in some species). This new morphological relationship may have been a primary anatomical adaptation that permitted subsequent hypertrophic development of the appendicular component and directly contributed to the evolution of a new functional modality for the caudo-iliofemoralis muscle complex. I hope to test this hypothesis for a myological correlate of a "form-function complex" (see Bock 1974) in a new study of this muscle complex in a sample of specimens from selected avian groups.

CONCLUSIONS

As Homberger (1980) mentions in her review of the "Nomina Anatomica Avium," our knowledge of avian anatomy is still incomplete in the sense of not having been checked and rechecked by countless researchers, and, indeed, there is a very real danger that inaccurate or incomplete anatomical descriptions may be accepted as authoritative, more so than in human or veterinary anatomy, for example. In the previous discussion of a series of anatomical variants of selected muscles, as exemplified in *Apteryx*, I have attempted to demonstrate some aspects of the "incomplete" status of avian anatomy based on (1) descriptive myology, (2) probable misidentification or misrepresentation of muscles, and (3) morphological variations in a muscle set that have not been thoroughly examined in terms of a form-function complex.

Studies of the musculature of the pelvic limb in birds should continue to be a source of information on anatomical variation in somatic muscle patterns among vertebrates if the proper anatomical questions are first proposed. Then the relative development of individual muscles and/or functional groups of muscles, muscle structure (pennation, fiber types, aponeuroses, innervation, etc.), and musculoskeletal parameters of form and function should all contribute to the informational value of anatomical studies and to the interpretation of anatomical variation at several levels of scientific inquiry (see Cracraft 1971, Helmi and Cracraft 1977, Raikow 1978, Zusi and Bentz 1978, for several different applications). Unfortunately, until very recently the nomenclature for avian anatomy, especially the musculature, has been a source of considerable confusion, but the standardization of the anatomical nomenclature should help to alleviate this problem.

What is the present status of our knowledge concerning the myology of the pelvic limb in *Apteryx* relative to that in ratites and carinates? Somehow, it seems ironic that a comment by T. J. Parker (1891: 103–104) on "deficiencies" in the original papers of Owen might still be applicable nearly 100 yr later: "It is a curious circumstance that whenever subsequent observers have had occasion to correct the original description of *Apteryx*, the result has been to show the bird to be less aberrant and more typically avian than it was considered to be by the distinguished anatomist [i.e. Owen] to whom we owe our first knowledge of its structure."

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I have attempted to verify the morphological relationships of the muscles described by any investigator cited, with one or more illustrations of the same in that text or some other related publication. I wish to thank W. J. Bock, J. Cracraft, S. L. Olson, R. J. Raikow, and R. L. Zusi for their respective critiques of a much longer and more detailed draft of this manuscript.

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MOVEMENTS AND ACTIVITIES OF RADIO-TRACKED BROWN-HEADED COWBIRDS

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ABSTRACT.—The social organization of a color-marked Brown-headed Cowbird (*Molothrus ater*) population was investigated during the 1978–1980 breeding seasons. Several members of the population were radio tracked, some in more than one season. Monogamous associations were established between males and females, and each pair maintained a large nonfeeding range. Females appeared to defend their nonfeeding ranges from other females, and males guarded females from other males. Most cowbird pairs that returned in successive years exhibited mate fidelity and site fidelity, although some evidence indicates that the former is a coincidental result of the latter. I propose that variations in the mating system of this species are primarily due to habitat differences and differences in the relative abundance of the cowbird and its hosts. *Received 8 May 1981, accepted 2 September 1981.*

THE Brown-headed Cowbird (*Molothrus ater*) is the most abundant cowbird in the United States and the best-studied member of its genus. Most investigations of this species have dealt with rates of brood parasitism and effects of parasitism on the reproductive success of hosts (e.g. Norris 1947; Walkinshaw 1949, 1961; Berger 1951; Wiens 1963; Rothstein 1976; Elliott 1978). In contrast, much less is known about the social relationships of cowbirds. The reasons for this relative dearth of information are twofold. First, cowbirds do not construct nests, so a convenient focal point for the observation of social activity is absent. Second, cowbirds range over large areas (Friedmann 1929, Nice 1937, Darley 1968), making continuous observation of individual birds quite difficult. Nice (1937), Laskey (1950), and Darley (1968) observed color-marked individuals, but only Darley followed a large number of birds over a broad area. Color-marking alleviates the problem of individual recognition but does not reduce the difficulties associated with locating and following cowbirds. This problem is especially acute with female cowbirds, which are more secretive than males.

These difficulties may have contributed to contrasting descriptions of social organization for this species, ranging from monogamy to promiscuity (Friedmann 1929, Nice 1937, Laskey 1950, Darley 1968, Rothstein 1972, Elliott 1980). Confounding the problem further is the likelihood that the mating system varies between geographic areas (Friedmann 1929, Elliott 1980).

This paper reports on a study of the movements and behavior of cowbirds, using color-marking and radiotelemetry. Radio tracking has been successfully employed in a number of investigations of passerines (e.g. Cochran et al. 1967; Bray et al. 1975a, 1979), and it is particularly suitable for use with a species as wide-ranging as the Brown-headed Cowbird.

METHODS

Capture and banding.—Most cowbirds were captured in mist nets or Potter traps placed around each of two artificial feeders. The feeders were 0.16 km apart and were located approximately 0.8 km from the Binghamton campus of the State University of New York. In 1978, trapping began on 22 April and continued through the end of June. In 1979, trapping started on 30 March and continued almost daily until 29 May. In 1980, trapping was conducted from 20 March through 16 June. Trapping was less intense in 1979 and 1980 than in 1978. All captured birds were individually marked with colored leg bands and were fitted with colored leg streamers 2.54 cm in length. Yearling and adult male cowbirds were distinguished on the basis of retention of juvenal underwing coverts in the former group (Baird 1958, Selander and Giller 1960). Yearling and adult females were not differentiated.

Radio tracking.—Field observations of the color-marked population revealed that birds that were lo-

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cal residents and appeared to be paired. If these were recaptured, they were fitted with transmitters (model SM1, AVM Instrument Co., Champaign, Illinois) with a Mallory Duracell RM-312T2 mercury battery power source. The birds were then released.

The radio transmitters were attached to the cowbirds by glueing them to the interscapular region of the spinal tract, just anterior to the points of articulation of the humeri. The birds were held in one hand in the manner illustrated by Raim (1978, Fig. 2). All the feathers in an area the size of the transmitter unit were cut to within 1–2 mm of the skin. The feathers were cut rather than pulled out, as the latter method reduces the retention time of the transmitter. Epoxy glue (Devcon 5 Minute Epoxy) was applied to the ventral surface of the transmitter, which was carefully placed onto the exposed area and held firmly for five minutes (longer if excess glue was applied). A few uncut feathers, just anterior and lateral to the transmitter, were glued to it to secure the unit further. Each transmitter-battery unit weighed approximately 2.5–3.0 g.

All of the cowbirds pulled at the transmitters initially, but most ignored them after a few hours. A few birds never accepted the transmitters and continued to peck at them until they became detached. Raim (1978) reports similar behavior. Many of the cowbirds had deeper wingbeats following attachment of the transmitters, but reaction time and flight speed did not appear to be affected. Transmitters remained on those birds that accepted them for 3–21 days, at which time they either fell off or were removed by me.

Most tracking was done in the morning and late afternoon when the birds were most active. Transmitter signals were received by a hand-held AVM Yagi antenna coupled to an AVM model LA 12 portable receiver. Tracking and behavioral observations were tape recorded in the field and later transcribed. Tracking locations were plotted on an aerial photograph of the study area. Only the nonfeeding locations of the birds were considered when plotting ranges. Movements to midday resting areas, where cowbirds from several ranges congregated, were excluded from consideration. One such resting area was located near my primary trapping site (Fig. 1). In 1979 birds from areas 1, 2, 4, 5, and 6 were known to rest there, as did several unidentified cowbirds. Likewise excluded were the locations of aggressive encounters in which birds were driven from the range of another pair. On occasion the signal of a tracked bird would disappear, reappearing a few minutes later. Most instances of this nature could be attributed to the signal being blocked by vegetation, the bird flying to the ground (thereby reducing the effective range of the transmitter), interference from citizens' band radios, and solar interference (especially near midday). I cannot eliminate the possibility, however, that some of these disappearances resulted from birds leaving their ranges for short periods of time, and such movements (if they occurred) are not plotted. Each nonfeeding range was determined by connecting the remaining outermost locations of a bird. The area of each range was calculated using a polar planimeter.

Birds from a particular range were assigned the letter M or F, which designated them as male or female, and a number corresponding to their range. Birds radio-tracked in more than one year retained the same number. Primed (′) numbers represent replacement birds.

Both resident and nonresident females were present in the study area. Resident females maintained nonfeeding ranges that overlapped those of neighboring females only slightly. These females were observed frequently. Nonresident females were rarely observed and never exhibited aggressive behavior in the study area. They were seen primarily at feeding areas. There was no evidence of nonterritorial resident females in my population, although Darley (1968) noted such females in his. Male cowbirds were designated as mated or unmated according to their relationships with the resident females. No attempt was made to catalog systematically all the resident unmated males, and a number of males remained unbanded throughout the study period.

RESULTS

Banding and sex ratio.—In 1978, 50 males and 38 females were banded, a male : female ratio of 1.32:1. In 1979, 38 males and 27 females were captured, a ratio of 1.41:1. These values are not significantly different from unity for the two years ($\chi^2 = 1.65$ and 1.88, respectively; $P > 0.05$ for both). In 1980, 45 males and 21 females were trapped. This male : female ratio of 2.14:1 is significantly different from unity ($\chi^2 = 8.74$, $P < 0.005$), as is the combined data for the three years ($\chi^2 = 10.09$, $P < 0.005$), which give an overall male : female ratio of 1.55:1. Thirteen yearling and 36 adult males were captured in 1978 (one male was not aged). In 1979 and 1980 these age classes had 11 yearlings and 27 adults and 13 yearlings and 32 adults, respectively, for a total of 37 yearling and 95 adult cowbirds.

Radio tracking.—Seven cowbirds were radio tracked in 1978, four females and three males. The nonfeeding ranges of these birds are shown in Fig. 1. Areas 1, 2, and 4 of Fig. 1 represent ranges that were identical for both a male and a female cowbird. These birds were considered to be paired. The fourth female also appeared to be paired, but, because her mate was unbanded, her status could not be determined with certainty.

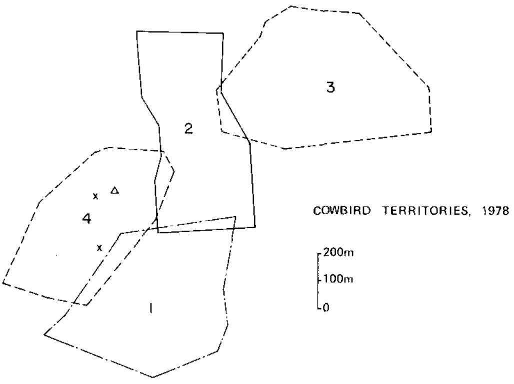

Fig. 1. Nonfeeding ranges of Brown-headed Cowbirds in 1978. X = trapping site. Triangle = midday resting area for cowbirds of several ranges.

Eleven birds were radio tracked in 1979 (Fig. 2). Pairs of birds were tracked in areas 2, 4, 5, and 6. Male members of pairs were followed in areas 8 and 9. A mated female was tracked in area 7. The male in area 1 was not radio tracked in 1979. Area 1 had few large trees to obstruct my vision, and I was able to follow his movements over most of his range. The areas where observations of this male were difficult are labeled as "proposed boundary," because few data were obtained at these locations.

Three birds are known to have been killed in 1979. F5 was taken by a predator on 21 April. Her mate was seen with a replacement female on 23 April, and this female (F5′) was subsequently captured and radio tracked. Her range appeared to be the same as that of F5. M6 and M9 were found dead on 11 May and 22 May, respectively. Each had been shot with a pellet gun. A second male (M6′) paired with F6; he was radio tracked and maintained a nonfeeding range identical to that of M6. Female F9 was subsequently guarded by an unbanded male whose range was not determined.

M8 was tracked for 71 min over 2 days before his transmitter malfunctioned. Observational data were used to supplement the tracking data in determining his range.

Two pairs of cowbirds tracked in 1979 had also been tracked in 1978. These birds settled in much the same areas as in 1978 and once again had identical ranges (Figs. 3 and 4). The male from the remaining pair (M1) returned and mated with a different female. His 1978 mate was not seen in the study area in 1979. The 1979 pair established themselves near the male's 1978 area (Fig. 5).

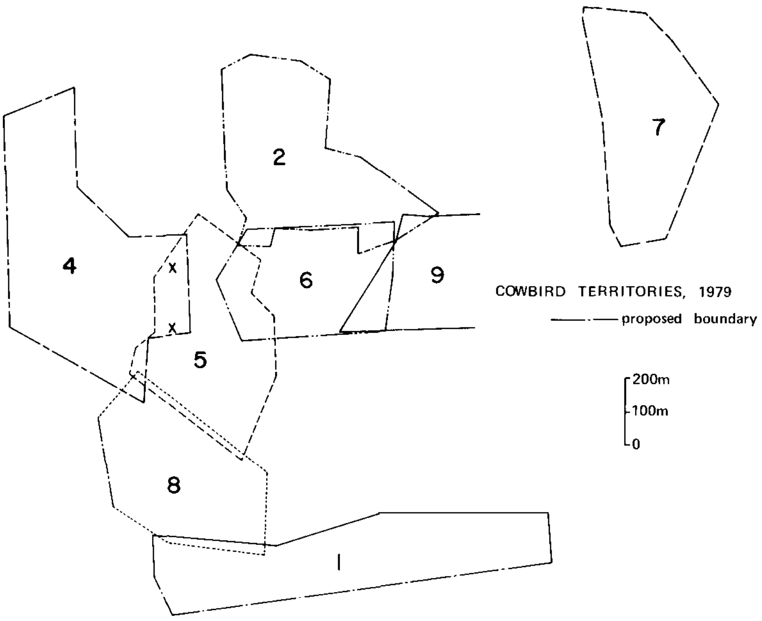

Fig. 2. Nonfeeding ranges of Brown-headed Cowbirds in 1979. "Proposed boundary" refers to areas in ranges 1 and 8 where data were sparse.

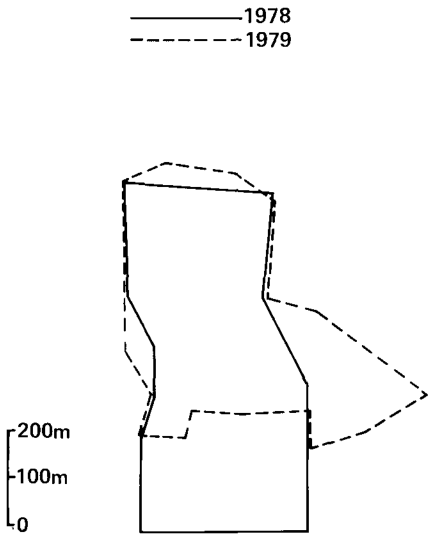

Fig. 3. Superimposed nonfeeding ranges of a cowbird pair (number 2 in Figs. 1 and 2) in 1978 and 1979.

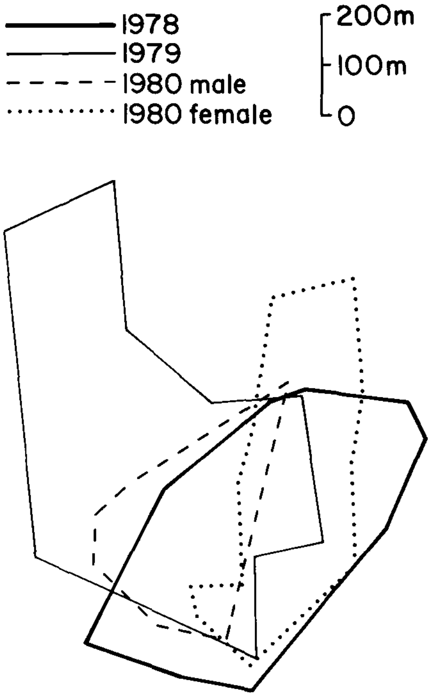

Fig. 4. Superimposed nonfeeding ranges of a cowbird pair (number 4 in Figs. 1, 2, and 6) in 1978–1980. In 1980 the male and female paired with different mates.

Tracking data for 1980 are shown in Fig. 6. Females were followed in areas 4 and 11. Both birds in areas 6 and 10 were tracked, but the data for M10 were lost due to equipment failure. Nonetheless, his range coincided with that of F10.

Two males and two females tracked in 1979 returned in 1980. One pair (M4-F4) returned for the third consecutive year. Instead of pairing and assuming identical home ranges, as they had done in 1978 and 1979, F4 settled with a new male in an area adjacent to the one in which M4 was located with a new female. Each of their 1980 ranges partially overlapped their 1979 ranges (Fig. 4). The range sizes for all birds, 1978–1980, are presented in Table 1.

Of the 12 males that were tracked during the course of this investigation, five were yearling birds and the rest were adults.

Pairing.—The evidence suggests monogamous associations between male and female cowbirds. Figures 1, 2, and 6 show that cowbirds limited their nonfeeding activities to large yet well-defined areas. The fact that certain males and females exhibited identical ranges implies that these birds were paired. On nine occasions both members of presumptive pairs had simultaneously active transmitters. Both signals were often found together and moved together throughout the ranges. The close association between pair members, resulting primarily from males assiduously following females (Darley 1968, Dufty 1981; see also below), accounts for the uniformity of range boundaries for males and females of pairs. Males accompainied females throughout much of the day, although there were extended periods in the mornings when females were stationary and alone, presumably searching for nests. For example, F4 was tracked for 1,371 min during the mornings of 13–18 June 1978, a time when both members of pair 4 had active transmitters. She was alone and relatively inactive on 25 occasions, for a total of 457 min ($\bar{x}$ = 18.28 ± 10.18 min, range = 7–48 min) or 33.3% of the time she was tracked.

The coincidental movement of the signals of a male and female does not preclude the possibility that birds without transmitters also accompanied them, but when both members of a tracked pair were visible there was no evidence of additional cowbirds of either sex in regular attendance. When a pair was not visible, I could usually detect the presence of other

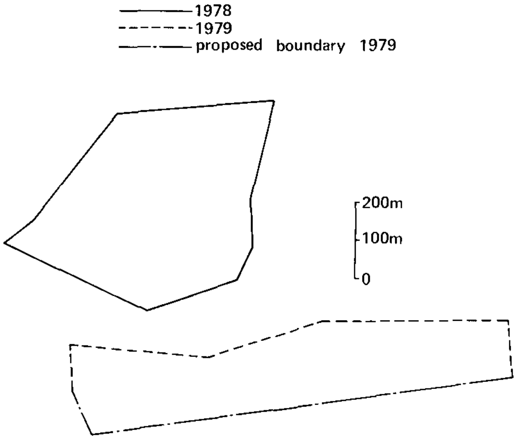

Fig. 5. Superimposed nonfeeding ranges of a cowbird pair (number 1 in Figs. 1 and 2) in 1978 and 1979. In 1979 the male paired with a different (untracked) female. He was tracked visually in 1979. "Proposed boundary" refers to areas where data were sparse.

TABLE 1. Sizes of the nonfeeding ranges of Brown-headed Cowbirds, 1978–1980.

Range number[a]	Size (ha) 1978	1979	1980
1	25.5	22.7	
2	22.8	21.1	
3	29.3		
4	20.5	29.7	
4a			9.9
4b			14.1
5		19.3	
6		15.6	33.2
7		18.1	
8		17.5	
10			11.0
11			15.3

[a] Range numbers correspond to those found in Figs. 1, 2, and 6.

cowbirds by differences in their vocalizations. These instances also occurred irregularly.

Further evidence that males and females were paired is presented in Tables 2 and 3. Table 2 shows the amount of time each female was seen with her presumptive mate only, with her mate and other males, and with other males only, in 1978 and 1979. Instances are considered only if the identities of both members of a pair were known. Some male mates had active transmitters, which could have made them easier to locate than unmarked males, thereby biasing the data. To avoid this bias, data are included only if the birds were visible, thus obviating the need for radio tracking in locating birds. Each female cowbird was seen more often with her mate only than with other males [Wilcoxon matched pairs signed-rank test (Siegel 1956), $T = 0$, $P < 0.01$]. Data for 1980 show a similar trend but are not presented, because many of the tracked birds' mates were not banded at the time of tracking, so sample sizes are small.

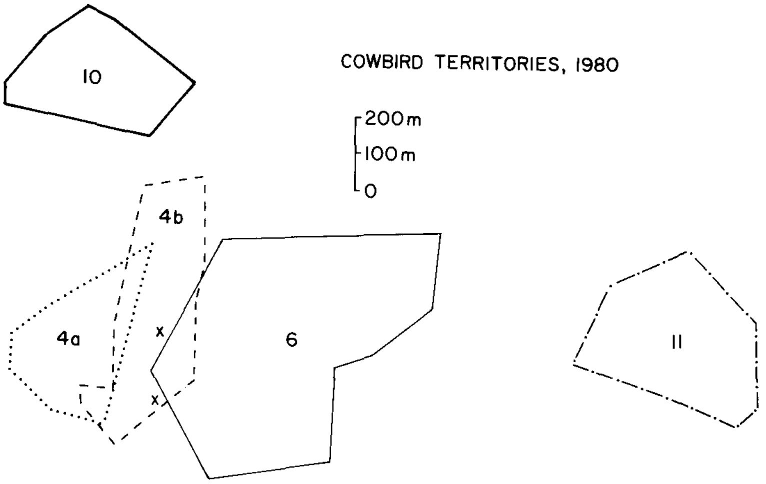

Fig. 6. Nonfeeding ranges of Brown-headed Cowbirds in 1980. The male (a) and female (b) from area 4 returned to their range of the previous 2 yr but had different mates.

TABLE 2. Time (min) that each female cowbird was seen in the presence of her mate, her mate and other males, and other males.

		Time seen with:		
Year	Cowbird $(n)^a$	Mate $(n)^b$	Mate and other males $(n)^b$	Other males $(n)^b$
1978	F1 (7)	53 (11)	7 (3)	20 (5)
	F2 (7)	530 (66)	295 (36)	15 (4)
	F4 (13)	163 (33)	53 (12)	1 (1)
1979	F2 (10)	125 (23)	147 (24)	8 (4)
	F4 (3)	25 (6)	11 (3)	24 (4)
	F5 (1)	29 (3)	1 (1)	0
	F5′ (2)	28 (4)	5 (1)	0
	F6 (2)	15 (4)	2 (2)	3 (1)

[a] Number of days of observation.
[b] Number of observation sessions.

TABLE 3. Time (min) that each male cowbird was seen in the presence of his mate, his mate and other females, and other females.

		Time seen with		
Year	Cowbird $(n)^a$	Mate $(n)^b$	Mate and other females $(n)^b$	Other females $(n)^b$
1978	M1 (7)	54 (14)	6 (1)	0
	M2 (6)	545 (71)	280 (27)	2 (1)
	M4 (14)	174 (39)	42 (6)	8 (3)
1979	M2 (9)	151 (27)	71 (14)	3 (1)
	M4 (3)	25 (6)	11 (2)	0
	M5 (8)	134 (13)	41 (3)	0
	M6 (4)	19 (6)	18 (3)	15 (3)
	M6′ (8)	28 (6)	15 (1)	7 (1)

[a] Number of days of observation.
[b] Number of observation sessions.

The analagous data for males are presented in Table 3. As with females, each male was seen more often with his mate only than with all other females combined ($T = 0$, $P < 0.01$). A male accompanied his mate and other females on feeding grounds and during territorial interactions between the females. If the mate of the other female was also present, the males would sing and display to each other. If the other female's mate was not present, the male would sing to the females or sit quietly nearby while the females interacted. When a paired male was with a female other than his mate, he would sing to her (if she was alone) or engage in a display bout with her mate.

"Following" behavior of males.—I have indicated above that mated males attempt to stay near their females. If such is the case, then males should follow their females when the latter take flight, while the converse should not necessarily occur. In testing this prediction, flights of pairs were recorded. When one member of a pair flew, the other member was watched to determine if he or she followed the first member within 10 s. Of 314 such flights, females flew first 239 times. Males followed females in 206 (86%) of these flights. Several instances in which male cowbirds did not follow females occurred when females made short flights into vegetation, possibly to begin nest searching. Males flew first 75 times, with females following on only 12 (16%) occasions. The difference between the tendency of males to follow females and females to follow males is significant ($\chi^2 = 129.22$, $P < 0.005$).

Aggressive behavior.—To determine whether or not male cowbirds defend their mates from other males, I observed the outcome of display bouts between guarding and intruding males in the presence of resident females. The departure of a male in advance of the female was scored as a defeat for that male. I scored 74 instances, involving 9 guarding males ($\bar{x} = 8.2 \pm 7.1$ instances/male, range = 1–22) and 101 intruders. The guarding males won 64/74 bouts (86%); thus, mated males were significantly more likely to win such bouts than were intruders ($\chi^2 = 39.42$, $P < 0.005$). Of the 10 cases in which guarding males flew off, four occurred early in the season, when guarding ability may not have been completely established. Two others occurred the day after a male (M4) had been fitted with a transmitter, perhaps while he was still adjusting to its presence.

Aggressive behavior between females was less regularly observed. I never saw a female guard her mate from other females. In the mornings, most female-female encounters were at territorial boundaries ($n = 51$), with fewer (16) occurring deep within a female's territory. In the afternoons cowbirds fed communally, either on lawns or elsewhere (e.g. horse pastures). Feeding sites were not defended, even those lying entirely within a female's range, and little aggressive behavior was recorded at these locations.

As might be expected in encounters between neighboring territorial females, there was often no clearly observable victor. The females would chatter and give aggressive bill-up displays to each other as they hopped from branch to branch. Eventually they would become separated, each toward her own territory, and the interaction would end. At other times the females would take flight in opposite directions or would fly together out of sight. Raim (1979) reports similar activities. Whereas the social relationships between males were readily discernable, such relationships between females were less obvious and may have operated at a more subtle level.

Removal of females.—Females from seven pairs were temporarily removed from the population in May 1979 and May 1980, in addition to the permanent removal of F5 by a predator in April 1979. These females were kept in isolation for 3–8 days. The male member of each pair confined his movements to the established nonfeeding range, and none was seen in association with a lone female up to the time their females were returned. On those infrequent occasions when a male was seen with a female, she was a neighbor in the company of her mate, and the encounters occurred at the boundary of the nonfeeding range or on communal feeding grounds. The females all returned to their respective territories upon release, and their mates resumed guarding behavior.

DISCUSSION

The skewed sex ratio of the captured cowbirds (1.55:1) is similar to the 1.5:1 ratio observed by Friedmann (1929) and Darley (1971). The imbalance in the sex ratio may be an artifact, because the male : female ratio of immature cowbirds is 1:1 (Hill 1976) and females are more secretive in their movements than males. Fankhauser (1971) and Searcy and Yasukawa (1981), however, have found that male cowbirds have a higher survival rate than do females. Furthermore, Darley (1971) and Burtt and Giltz (1976) have shown that female cowbirds are retrapped significantly more often than are males, suggesting that the proportion of males in the population may actually be underestimated.

Despite my bias of deliberately selecting males that had been tracked in previous years, almost half ($^5/_{12}$) of the paired radio-tracked males were yearling birds, breeding for the first time. This is not significantly different from their representation in the population as a whole ($\chi^2 = 0.44$, $P < 0.05$). Payne (1965) and Darley (1968) also reported that yearling males breed successfully. This contrasts with yearling males of polygynous icterid species, such as the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) and the Red-winged Blackbird (*Agelaius phoeniceus*), where juvenile males either do not breed or have reduced reproductive success (Willson 1966, Searcy 1979).

The cowbirds that were radio tracked showed nonfeeding ranges that averaged 20.4 ha in size. These ranges were identical for both members of a pair. Darley (1968) mapped the nonfeeding ranges of color-marked cowbirds and found that the male member of a pair usually had a larger range, which overlapped that of the female. The nonfeeding ranges averaged 4.5 ha for his females and 6.6 ha for his mated males, considerably smaller than the ranges in my population. It is possible that Darley was not able to track his birds visually over all parts of their ranges, resulting in smaller apparent ranges than would have been found by radio tracking. Alternatively, the smaller ranges of the cowbirds studied by Darley may have reflected a higher population density in his study area. This would increase the cost of defense of the ranges (Brown 1964) and reduce the size of each range. Changes in territory size in populations with different densities have been found in several species, such as the Song Sparrow (*Melospiza melodia*), Dickcissel (*Spiza americana*), and Great Tit (*Parus major*) (Tompa 1962, Zimmerman 1971, Krebs 1971).

In addition to having identical nonfeeding ranges, paired cowbirds spent significantly more time in the presence of their mates than in the presence of other cowbirds of the opposite sex. This was effected primarily by the male, who attended the female diligently, following her as she moved through her territory and defending her from the approach of other males. Guarding behavior may reduce the risk that a female will engage in extra-pair copulations, for solitary male cowbirds presented with a model of a female and tape-recorded female vocalizations rapidly approach the model and occasionally attempt to copulate with it (Dufty 1981). Energetically, it may be more feasible for a male to guard his mate than to attempt to patrol her entire nonfeeding range (Conder 1949, Brown 1964), especially because the skewed sex ratio of breeding cowbirds suggests that males must compete for access to females (cf. Emlen and Oring 1977). The severity of the intermale competition for females is demonstrated by the results of the female removal experiment. None of the males whose mate had been removed was able to secure a second female within the time constraints of the experiment. A male whose mate was taken by a predator did obtain a second female, although this occurred early in the season when some females may still have been searching for territories.

Females, in contrast to males, do appear to defend their nonfeeding ranges from other same-sexed conspecifics, resulting in minimal overlap of territories of neighboring females. Spacing-out of adjacent females is not simply due to mutual avoidance, for female-female encounters were characterized by aggressive rather than avoidance behavior. The aggressive response of these females to simulated female intruders further supports this hypothesis (Dufty 1981). Darley (1968) has suggested that female cowbirds defend access to host nests. Such territorial behavior may increase the reproductive success of individual female cowbirds by reducing the amount of multiple parasitism, thereby reducing competition between their nestlings and those of other females.

The integrity of the pair bond between cowbirds was maintained in successive breeding seasons, with pairs exhibiting site fidelity. Friedmann (1929) felt that his birds returned to the same territories each spring, although he worked with unmarked birds. Nice (1937) reported faithfulness to breeding sites in her color-banded cowbirds. Darley (1968) also noted that pairs occupy the same (or overlapping) nonfeeding areas in successive years. Additional reports of site fidelity can be found in Laskey (1950), Hunt (1977), and Kennard (1978).

The significance of a durable pair bond in cowbirds is unclear. In long-lived species, birds that have paired in previous years have higher reproductive success than newly formed pairs. Coulson (1966) found that Black-legged Kittiwakes (*Rissa tridactyla*) are able to raise more young if they have bred together previously. Likewise, both members of Song Sparrow, Skylark (*Alauda arvensis*), and Great Tit pairs will return to their previous nesting area if they successfully fledged young (Nice 1937, Delius 1965, Harvey et al. 1979). It is unlikely that cowbirds are afforded a similar advantage, because cowbirds perform no parental care. Fledging success in cowbirds is determined by the timing of egg deposition, the reaction of the host to the cowbird egg, and any subsequent nestling-foster parent interactions, factors that would appear to be little affected by the presence or absence of a lasting pair bond.

Breeding-site fidelity may play a more prominent role in the determination of reproductive success in individual cowbirds. Males form hierarchies, with the dominant male pairing with the female of that particular area (Laskey 1950, Darley 1968). Copulation with a female may be largely restricted to the dominant male (West et al. 1981), although early in the season, when the hierarchy may not be firmly established, other males may copulate with her (Darley 1968). Therefore, dominance in an area probably translates into high reproductive success relative to subordinate male cowbirds.

Fidelity to an area where a male has successfully bred in previous years may facilitate acquisition of a dominant position in succeeding seasons. In the Red-winged Blackbird, males who have had prior reproductive experience in a territory return to that territory the following year and readily establish themselves therein (Nero 1956, Searcy 1979). Similarly, site fidelity in male cowbirds may have evolved as a result of intrasexual selection pressure, and a male's faithfulness may be to his breeding area and not to his female. Three observations are consistent with this hypothesis. Male M1, whose mate did not return in 1979, paired with a new female, yet he maintained a nonfeeding range juxtaposed to his 1979 range. Furthermore, when females were temporarily removed from the population, none of the males abandoned their ranges. Finally, the members of a pair (M4-F4) that had bred together for two consecutive years on the same territory consorted with different mates the third year, each on a different part of the old territory, indicating that site fidelity may take precedence over mate fidelity.

Data from Darley (1968) also support the view that successful breeding facilitates site fidelity. Ten of 12 of his paired males returned to the study area in the second year; only 2 of 9 unmated resident males did so.

The apparent mate fidelity results from coincidental site fidelity on the part of the females. Females defend their territories, as shown by the results of playbacks of cowbird vocalizations to resident females (Dufty 1981). They do not desert their territories if their mates are killed; females F6 and F9 both remained in their territories and paired again after their mates died. This is consistent with Darley's (1968) data. As with males, prior breeding experience in an area may ease a female's subsequent establishment in that area. Additionally, because females spend much time searching for nests (Friedmann 1929), familiarity with territories could enhance the efficiency of their nest-searching activities, allowing them to find more nests or to spend more time in other activities such as territorial defense or feeding. Therefore, intrasexual pressure on males to obtain mates and on females to obtain breeding territories probably results in site fidelity in both sexes and, secondarily, in mate fidelity. Nolan (1978) similarly concluded that mate fidelity in Prairie Warblers (*Dendroica discolor*) occurs coincidentally, a result of site fidelity on the part of both members of a pair.

While the data strongly suggest a monogamous relationship between male and female Brown-headed Cowbirds in my population, the supposition of monogamy must be tempered by the fact that no copulations were observed during this study, so the actual mating pattern is unknown. Because other species thought to be monogamous or polygynous have been shown to be more promiscuous than previously suspected (Bray et al. 1975b, Burns et al. 1980), a final conclusion regarding monogamy in these cowbirds must await information regarding mating patterns in the wild.

MATING SYSTEMS IN THE BROWN-HEADED COWBIRD

Territoriality is thought to have evolved through competition for a limiting resource (Brown 1964). If the resource is economically defensible, then territorial behavior may develop, that is, the cost to the bird of securing the resource must not outweigh the benefits. Competition for resources varies directly with the density of the population and inversely with the abundance of the defended resource. Emlen and Oring (1977) have applied Brown's ideas to the evolution of mating systems. They feel (p. 222) that "considerable lability in mating systems is . . . expected between different populations of a given species in different environmental or density situations."

The mating system of the Brown-headed Cowbird is not identical throughout its range. The system I have described is similar to that reported by Friedmann (1929) in New York and by Darley (1968) in Ontario, yet Elliott (1980) has shown that cowbirds are promiscuous in prairie habitats. Differences in population size and habitat may be crucial factors in explaining these contrasting breeding systems.

Cowbirds apparently entered the United States through Texas and the Prairie States (Friedmann 1929) and extended their range eastward with the removal of large tracts of woodland that had served as a barrier to dispersal (Mayfield 1965). The Prairie States still have the highest densities of cowbirds. Surveys show that the population densities of cowbirds in Oklahoma, Kansas, and Nebraska are 2–3.5 times higher than those in New York, and the difference is increasing (Van Velzen 1972, Dolbeer and Stehn 1979). In contrast, Wiens (1973) has shown that overall species diversity and population density in the open grasslands of the Prairie States is significantly lower than in the shrub/forest ecosystems of the Northeast. Thus, there is a higher density of breeding cowbirds competing for relatively fewer host species in the grasslands of the Prairie States than in the shrub/forests of New York. Competition in the grasslands would be further increased by the fact that many of the parasitized nests are located on the edge of the grasslands in shrubs or thickets, while those in the open expanse of the grasslands are relatively free from parasitism (Wiens 1963). Similar occurrences have been noted in open fields of other localities (Berger 1951; Best 1978, Fig. 4; Gates and Gysel 1978; Gochfeld 1979).

The relatively low cowbird population in the Northeast, coupled with the more abundant supply of host nests, could make defense of these nests profitable for female cowbirds in terms of reproductive success. McGeen (1972) and Elliott (1978) have shown that high levels of multiple parasitism reduce cowbird fledging success, so territoriality in female cowbirds could act to reduce competition between nestling cowbirds. In prairies, where competition from other females may be keener and the supply of nests available for parasitism lower, females may undergo a kind of "scramble" competition. That is, they may not be able to defend successfully an area from all other females and still locate enough nests in which to lay eggs. Under these circumstances they would be expected to abandon territoriality and simply lay in whatever nests they find. A similar situation occurs in other species, in which territorial behavior is reduced or abandoned when resources are not economically defensible, yet exclusive territories are maintained when the cost of such maintenance is low (Ewald and Carpenter 1978, Myers et al. 1979, Ewald et al. 1980).

Females in the Northeast are able to confine their nonfeeding activities to areas that are small enough that a single male cowbird is dominant in each. This results in monogamous associations between the birds. In contrast, Elliott (1980) reports that males in the prairies do not guard females and do copulate with more than one female. As argued above, females in prairie habitats may travel more widely than those in the Northeast, and a male cowbird may not be dominant in all parts of any given female's range. Because males may not be able to defend females from other males under these circumstances, males may maximize their reproductive output by adopting the alternate behavior of copulating with those females that enter the area where they are dominant. According to this interpretation, male cowbirds in the Prairie States should have smaller ranges than females.

As a consequence of these presumed differences in cowbird spatial patterns, certain predictions can be made regarding the deposition of cowbird eggs in the Northeast and Prairie States: (1) If females exclude same-sexed conspecifics from breeding areas in the Northeast, then the cowbird eggs found in any one territory should be similar to each other (indicating that they were laid by the same female), yet different from eggs found in adjacent territories. Remarks by Friedmann (1929:176) support this prediction, although no data are presented. Exceptions should occur at areas of territorial overlap, where eggs from neighboring birds may be found. In contrast, (2) local, parasitized nests in the Prairie States should contain dissimilar cowbird eggs, reflecting a lack of territorial behavior in females. Finally, (3) if territoriality functions to increase a female's reproductive success by limiting multiple parasitism, there should be relatively fewer cases of multiple parasitism involving two or more females in the Northeast than in the Prairie States.

Multiform mating systems have been reported in a number of avian species (Armstrong 1955, Case and Hewitt 1963, Verner 1964, Carey and Nolan 1975, Balfour and Cadbury 1979). Such variability may promote the efficient use of limited resources, such as mates (for male cowbirds) and host nests (for female cowbirds), and it provides these organisms with a certain amount of flexibility in their responses to differing demographic and/or environmental circumstances.

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An **International Symposium on the Tamaulipan Biotic Province** will be held at La Quinta Royale Motor Inn, Corpus Christi, Texas, on **28–30 October 1982.** The symposium will emphasize all ecological aspects of the biome: vegetation, invertebrates, vertebrates, ecological structure and function, biological resources (use and effects), and management. Abstracts of contributed papers are due 1 August 1982; abstracts for invited papers must be received by 1 September 1982. For information on the program, contact **Gene W. Blacklock, Curator, Welder Wildlife Foundation, P.O. Drawer 1400, Sinton, Texas 78387** or **David Riskind, Head, Resource Management Section, Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, Texas 78744.** For information on registration, contact **Jimmie R. Picquet, Director, John E. Conner Museum, Texas A&I University, P.O. Box 2172, Kingsville, Texas 78363.**

The joint **8th International Conference on Bird Census Work** and the **6th Meeting of the European Ornithological Atlas Committee** will be held at Newland Park College, Chalfont St. Giles, Buckinghamshire, United Kingdom, on **5–9 September 1983.** The conference will include papers on validation and testing of census methods, application of census techniques to bird community studies within and between habitats, description of vegetation and habitats for use in ornithological studies, atlas studies, and data processing methods. For further information, contact **R. J. Fuller, British Trust for Ornithology, Beech Grove, Tring, Hertfordshire, HP23 5NR, United Kingdom.**

EFFECT OF HABITAT DECIMATION ON RING-BILLED GULL COLONY- AND NEST-SITE TENACITY

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ABSTRACT.—Colony-site tenacity and nest-site tenacity have been documented in several larids, but the proximate factors affecting fidelity remain poorly understood. We examined the effect of severe breeding-habitat alterations (bulldozing) on site tenacity in Ring-billed Gulls (*Larus delawarensis*). Return rates of wing-tagged adults were similar in bulldozed and unchanged parts of the colony site. In bulldozed areas, however, most ring-bills abstained from nesting; those that did breed showed an increased tendency to move to a different nest site. *Received 14 April 1981, accepted 31 August 1981.*

FIDELITY to a previously used nesting area has been demonstrated or hypothesized for many bird species (see Greenwood 1980 for partial review). In colonially nesting birds, the area to which a bird returns from one breeding season to the next may be as large, and relatively imprecise, as a colony site (colony-site tenacity) or as precise as a specific nest site (nest-site tenacity).

Several larids have been subjects of investigations of colony-site tenacity and/or nest-site tenacity. Austin (1940) documented a well-developed tendency toward colony-site tenacity in Common Terns (*Sterna hirundo*), Arctic Terns (*S. paradisaea*), and Roseate Terns (*S. dougallii*). He subsequently reported (Austin 1949) that 86.2% of 115 Common Terns bred within about 9 m of their former nest site. Coulson and White (1958) noted that breeding Black-legged Kittiwakes (*Rissa tridactyla*) showed strong attachment to the colony site at which they had nested previously, but that 39.5% changed nest sites between years. Vermeer (1963) found that most (81.0%) Glaucous-winged Gulls (*Larus glaucescens*) nested within about 5 m of their previous site. Herring Gulls (*L. argentatus*) reportedly show a strong tendency to return to the vicinity of previously used nest sites (84% to same sub-colony, Chabrzyk and Coulson 1976). Franklin's Gulls (*L. pipixcan*) were reported to visit the colony site where they had nested in previous years, but after obtaining mates they often moved to a different site (Burger 1974). Nest-site tenacity also was suggested for this species (op. cit.).

For Ring-billed Gulls (*L. delawarensis*) nesting on the Great Lakes, Ludwig (1974) suggested that little, if any, attachment was shown to colony sites of various stabilities. Southern (1977) documented the existence of strong colony-site tenacity in this species at the stable Rogers City Calcite site. Recently, we reported that 96.7% of 152 adult Ring-billed Gulls returning to the Rogers City site were faithful to the same colony subdivision, and most birds bred within 3 m of their previous year's nest site (at least 69.5%, $n = 59$, Southern and Southern 1979). Blokpoel and Courtney (1980) reported similar results at another Great Lakes colony site. Of the 83 banded ring-bills they resighted, 71 (85.5%) nested in the same colony sub-area for 2 yr. In this case, at least some of the birds that changed areas were forced to move, because their previous site had been inundated.

Although the existence of colony- and nest-site tenacity has been demonstrated in several larid species, investigations of the proximate factors influencing tenacity have been limited. Chronological age and breeding experience have been convincingly shown to correlate with increasing degrees of site attachment (Austin 1940, Coulson and White 1958, Blokpoel and Courtney 1980). Other factors, such as predation, low reproductive success, and changes in habitat, have been implicated in causing breakdowns of tenacity (e.g. McNicholl 1975, Erwin 1977, Conover and Miller 1978). In spite of the obvious negative impacts of these factors, however, there are several accounts of continued re-use of adversely affected sites (e.g. Austin 1940, 1949; Southern and

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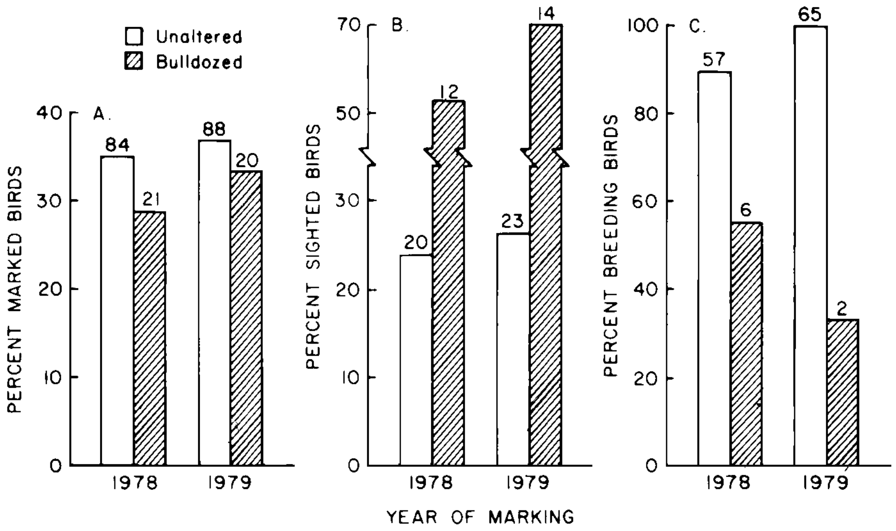

Fig. 1. The numerals above histogram columns indicate the number of birds each represents. A. Proportion of marked birds from bulldozed and unaltered areas that were resighted at the Calcite colony in 1980. B. Proportion of resighted birds, from bulldozed and unaltered areas, that did not nest in 1980. C. Proportion of birds resighted as nesters in 1980, from bulldozed and unaltered areas, that nested in the same subdivision as in previous years.

Southern 1978; Southern et al. 1979; Buckley and Buckley 1980; Petersen 1980).

In 1980, we addressed the question: does decimation of the breeding habitat affect nest-site tenacity in Ring-billed Gulls and, if so, in what way? Our experimental setup was provided for us by the unexpected bulldozing of parts of our study site. By observing the reactions of Ring-billed Gulls encountering these unusual habitat changes, we hoped to gain a better understanding of the influence of such changes on nest-site tenacity in this species. The changes caused by heavy equipment might simulate the type of habitat alterations that ring-bills could experience as a result of ice or waves scouring low-lying colony sites.

Study Area and Methods

This study was conducted at the Calcite colony near Rogers City, Michigan (Presque Isle County, 45°N, 83°W). A manmade peninsula that serves as a breakwall for the harbor area of U.S. Steel's calcite plant has also served as a colony site for nesting gulls for several decades.

In 1978–1979 we captured adult Ring-billed Gulls during mid- to late-incubation by means of a cannon-net. Cannon-netting was conducted only in favorable weather and with a minimum of five persons present to expedite the procedure. Each captured bird was outfitted with a standard U.S. Fish and Wildlife Service band and a patagial tag carrying a unique code (Southern 1971). We tagged 313 birds in 1978 and 395 in 1979.

We designated and marked subdivisions of the colony on the basis of permanent physical structures, e.g. harbor markers. Subdivisions varied widely in shape and size, averaging about 600 m^2 (mapped in Southern and Southern in press). We observed marked birds from a car, serving as a blind, parked along gravel roads, which run throughout the colony, and noted the subdivisions in which marked birds were sighted and/or nested. Observations were made on a near daily basis during 13 May–13 June 1978, 8–23 May 1979, and 10 May–27 June 1980.

During the fall of 1979, when breeding birds were not present, portions of the colony site were covered with 15–30 cm of fill and graded. These alterations affected some areas that had been used for nesting by birds wing-marked in 1978 and 1979. All vegetation was eliminated in these areas and a hard-packed, bare limestone substrate resulted. In contrast, unaltered areas supported ground cover and weedy vegetation during the summer (e.g. *Capsella*, *Chenopodium*).

Results

Marked birds that had nested previously in bulldozed and unchanged areas were sighted at the Calcite colony with similar frequencies in 1980 (Fig. 1A; marked 1978, $\chi^2 = 0.98$, $\nu =$

TABLE 1. Comparison of 1979 and 1980 nest censuses and mean clutch sizes in bulldozed and unaltered areas.

	Unaltered	Bulldozed
Number of nests		
1979	5,625	1,415
1980	6,495	1,242
Change	+15.5%	−12.2%
Mean clutch size		
1979	2.68	2.64
1980	2.61	2.64
Change	−2.6%	0

1, $P = 0.32$; marked 1979, $\chi^2 = 0.25$, $\nu = 1$, $P = 0.62$). Overall resighting rates were low in 1980 (marked 1978, 31.9%; marked 1979, 33.9%). We suspect human activities, particularly harassment and killing of birds away from the colony site, were partially responsible. A local outbreak of histoplasmosis, associated with the colony site, had evoked sharp public reaction against the gulls. It is unlikely, however, that any one group of birds was affected by these factors to a greater extent than others.

Of those birds we recorded at the colony site in 1980, significantly more from bulldozed areas did not breed in the 1980 season (Fig. 1B; marked 1978, $\chi^2 = 6.93$, $\nu = 1$, $P < 0.01$; marked 1979, $\chi^2 = 13.92$, $\nu = 1$, $P < 0.01$). We designated a bird as a nonbreeder if we never saw it copulating, attending a nest or chicks, or repeatedly defending a territory. Because our sample of tagged birds was distributed throughout the colony, we had ample opportunity to sight birds in all subdivisions.

Nonbreeding birds from bulldozed and unaltered areas seemed to differ in their movements at the colony, although statistically significant differences were not shown ($\chi^2 = 3.19$, $\nu = 1$, $P = 0.07$). Nonbreeders from unchanged areas were sighted frequently (33 times) in the vicinity of their old nest site (i.e. same subdivision), but not uncommonly (14 times) elsewhere in the colony. Birds from bulldozed areas were seen near and away from their old sites equally often (15 times each).

Figure 1C illustrates the tendency of those birds that did breed in 1980 to nest in the same subdivision they had used the preceding year. Lower proportions of breeding birds nested again in bulldozed areas than did so in unaltered areas (Fig. 1C; marked 1978, $\chi^2 = 8.32$, $\nu = 1$, $P < 0.01$; marked 1979, $\chi^2 = 45.92$, $\nu = 1$, $P < 0.01$).

Nest-census and clutch-size data for 1979 and 1980 are compared between bulldozed and unaltered portions of the colony site in Table 1. Although the total number of nests in bulldozed areas declined between years, more than 1,200 pairs bred in these areas in 1980. Along with the unchanged clutch size between years, this would seem to indicate that the altered habitat was suitable for nesting.

We have very little information on the effect of habitat changes on the pair bond. Of five marked pairs identified in 1979 from unaltered areas, four remained together in 1980. One out of three pairs from changed areas did not reunite in 1980. These samples are not adequate for drawing conclusions.

Male and female Ring-billed Gulls showed similar degrees of site tenacity. Of 24 birds identified as females (Southern 1981), 3 (12.5%) changed subdivisions in 1980; 2 of the 3 were from bulldozed areas. Similarly, 13.3% of 45 males changed subdivisions; 3 of these 6 birds were from disturbed areas. Our sample sizes are not sufficient for determining whether or not one sex more readily deserted bulldozed areas than the other.

DISCUSSION

Severe breeding-habitat alterations (bulldozing) affected Ring-billed Gulls in the following way. Birds that had nested previously in areas bulldozed in fall 1979 were seen at the colony in 1980 as frequently as those from unchanged areas, but their tendency to breed was reduced significantly. Among those birds from disturbed areas that did breed, relocation to a different colony subdivision occurred with greater than expected frequency. Ring-bills that encountered a drastically changed local environment upon arrival at the colony and did not breed in 1980 were equally likely to be sighted near their old site or in other parts of the colony.

It appears that bulldozing somewhat reduced the attractiveness of the habitat to returning gulls. The number of nests in bulldozed areas decreased between 1979 and 1980, while increasing in unaltered areas. Bulldozed areas were more open than unaltered areas, and this may have contributed to an unfavorable reaction on the part of some birds.

Over 1,200 pairs did nest in bulldozed areas, but most marked birds familiar with those areas moved or did not nest. This implies that many birds breeding in disturbed areas may have been immigrants. Some faithful, but nonbreeding, marked birds remained near their prior sites throughout the season, and some occasionally defended territories. By their presence, these tenacious ring-bills might have attracted newcomers that perceived no change in the habitat and proceeded to breed.

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PARENTAL FEEDING OF NESTLING YELLOW WARBLERS IN RELATION TO BROOD SIZE AND PREY AVAILABILITY

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Abstract.—The feeding by adult Yellow Warblers (*Dendroica petechia*) of nestlings in broods of 3, 4, or 5 young was studied during two breeding seasons on the forested dune ridge near Delta, Manitoba. Broods of 2-day-old young were selectively fed geometrid larvae by the adults, and broods of 8-day-old young were selectively fed chironomids and geometrid and other Lepidoptera larvae. The diet varied among broods of 3, 4, and 5 young at both ages, but this variation did not appear to affect the growth rates of the young. The total weight of items brought per half hour increased with brood size among broods of 2-day-old young. Broods of four 8-day-old young were fed the greatest amount of food. The diet of the nestlings is contrasted with the diet of adult Yellow Warblers observed in the same locality. *Received 15 October 1980, accepted 19 October 1981.*

The Yellow Warbler (*Dendroica petechia*), along with six other species of primarily insectivorous passerines, nests densely on the forested dune ridge that separates Lake Manitoba from the Delta Marsh, Manitoba. Both the adults and nestlings of the species studied so far in this area are apparently sustained by a superabundant food resource, adult midges (Diptera: Chironomidae) (Busby and Sealy 1979, Biermann 1980, Sealy 1980). The greatest demand on the food resources in the ridge community probably occurs during the period when the young are being reared. It is important, therefore, to determine the diets of nestlings of the species in this community in relation to the food resources that are available at this time. We did this for the Yellow Warbler, and we examined the rates at which adults fed their young in broods of 3, 4, and 5 at two ages. To determine the effects of any feeding differences that might have been observed, we also measured the growth rate of the young. The diet of the nestlings relative to the prey available was also contrasted to that of adult Yellow Warblers studied on the same area by Busby and Sealy (1979). As the diet of nestlings of most parulid species is poorly known, beyond the general knowledge that they are insectivorous, our study fills in a gap for the Yellow Warbler in one area.

Methods

We studied parental care in a densely nesting population of Yellow Warblers during the summers of 1978 and 1979 on a portion of the forested dune ridge that separates Lake Manitoba from the Delta Marsh, about 5 km west of Delta (50°11'N, 98°19'W), Manitoba. Willows (*Salix amygdaloides* and *S. interior*), Manitoba maple (*Acer negundo*), and green ash (*Fraxinus pennsylvanica*) account for over 95% of the tree flora and provide a forest canopy about 10–14 m in height (see MacKenzie 1979). The prominent shrubs are elderberry (*Sambucus pubens*), dogwood (*Cornus stolonifera*), and raspberry (*Rubus ideaus*) (see Goossen 1978, Busby and Sealy 1979).

We located 139 active Yellow Warbler nests and recorded their contents each day during egg-laying and every 3–4 days thereafter. Observations were made at 19 nests with broods of 3, 4, or 5 young on day 2 (young young, YY) and day 8 (old young, OY) after the first chick in each brood had hatched. At 10 nests at least one parent was color-banded, at 5 nests neither parent was banded, and at the other 4 nests at least one parent was aluminum banded. Adults at each nest were separable by plumage differences.

Four nests of each of the three brood sizes at each age were observed (except that 3 nests with broods of five 8-day-old young and 7 nests with broods of three 2-day-old young were observed). Most of the nests observed were less than 2 m above the ground. Observations were made from a blind placed 1–2 m from the nest the day before observations were begun, at four times of the day: 0630–0830, 1000–1200, 1530–1730, and 1830–2030 (CDT). Observations spanned 12 June to 1 July in 1978 and 20 June to 19 July in 1979. Parental activities at or near the nest and the number and identity of prey items fed to the young were recorded. Large insects that protruded from the parents' bills could be identified, but small items could not. Therefore, the prey we identified were biased toward larger sizes. Items brought were unidentifiable in 347 of 1,211 feeding trips observed,

TABLE 1. Feeding rates and food loads (mean ± SE) of Yellow Warbler parents.

Age and number of young		Trips/half hour		Items/trips	
		Males	Females	Males	Females
3YY[a]	(48)[b]	1.9 ± 0.2[c]	1.0 ± 0.2	1.2 ± 0.1	1.2 ± 0.1
4YY	(32)	2.6 ± 0.2[c]	1.6 ± 0.2	1.3 ± 0.1	1.2 ± 0.1
5YY	(36)	3.1 ± 0.3[d]	0.9 ± 0.3	1.2 ± 0.1[d]	1.0 ± 0
3OY	(32)	3.8 ± 0.5	3.4 ± 0.2	1.9 ± 0.1	1.5 ± 0.1
4OY	(31)	5.2 ± 0.5[c]	2.7 ± 0.4	2.6 ± 0.1	2.2 ± 0.2
5OY	(32)	4.2 ± 0.3[d]	5.6 ± 0.5	1.5 ± 0.1[c]	1.2 ± 0.1

[a] YY (young young) refers to 2-day-old young; OY (old young) refers to 8-day-old young.

[b] Number of half-hour observation periods in parentheses.

[c] $P < 0.01$ between males and females.

[d] $P < 0.025$ between males and females.

due in part to their smaller size, but also because the parents' positions while feeding the young obscured our view.

In 1979, 27 8-day-old nestlings were collected, and 70% ethanol was injected immediately into their esophagi. The stomach contents were removed within an hour and stored in ethanol. Food items were identified later in the laboratory using a variable-power microscope. Intact prey items were few in the samples, but head capsules, thoraxes, wings, occipital rings, and mandibles could be identified to order and often to family. This method probably biases results toward insects with thick hard coverings. The prey items observed being fed were compared to the prey items in stomachs to assess potential bias.

The foliage arthropod fauna of a 100-m line transect of a portion of the study area was sampled using a standard insect sweep net, in the manner described by Busby and Sealy (1979). They found that this method yielded representative samples when assessing the availability of arthropods to adult Yellow Warblers on this study area. The fauna was sampled in the morning and evening of every fifth day during the observation periods. The samples were sorted and identified to order or family and grouped into five categories to permit comparison with the prey being fed to the nestling warblers. These groups were: Chironomidae and Culicidae (midges and mosquitoes), Geometridae larvae (inchworms), all other Lepidoptera larvae, all other Diptera, and all other insects and arthropods.

The dry weights (to the nearest 0.1 mg) of the separate samples of midges, mosquitoes, and larvae were determined after being oven-dried at 60°C for one week. The two groups of larvae were then combined, and the protein content of the larvae and the chironomid and culicid samples was determined by the Manitoba Department of Agriculture.

Yellow Warbler nestlings in randomly chosen nests were weighed to the nearest 0.1 g between 2030 and 2130 (CDT) on a triple-beam balance. Nestlings could be weighed until day 6 post-hatching, after which they jumped out of the nest following handling.

Statistical tests used include analysis of variance (ANOVA), linear regression, Chi-square, and Wilcoxon sign rank test. The level of significance used was $P \leq 0.05$.

RESULTS

Feeding rates and food loads.—Time of day had no effect on the feeding rate of adult Yellow Warblers with young of either age. Broods of five 2-day-old young were fed significantly more often by males than were smaller broods (Table 1). Males with 8-day-old young fed broods of 4 young more often than broods of 5 or 3. Among females, the only significant result was that broods of five 8-day-old young were fed more often than were smaller broods [(two-way ANOVA: males with YY-brood size, $F(2, 104) = 6.16$; time of day, $F(3, 104) = 2.47$; males with OY-brood size, $F(2, 83) = 2.94$; time of day, $F(3, 83) = 0.71$; females with YY-brood size, $F(2, 104) = 2.52$; time of day, $F(3, 104) = 1.40$; females with OY-brood size, $F(2, 83) = 11.04$; time of day, $F(3, 83) = 2.30$].

The number of items brought per trip by males and females with 2-day-old young was constant throughout the day and did not vary among the different brood sizes [Table 1; two-way ANOVA: males—brood size, $F(2, 229) = 0.77$; time of day, $F(3, 229) = 0.76$; females—brood size, $F(2, 76) = 1.43$; time of day, $F(3, 76) = 1.50$]. Males feeding 8-day-old young brought the largest loads to broods of 4 (Table 1) and generally brought larger loads in the early morning and smaller loads in the late afternoon [two-way ANOVA: brood size, $F(2, 273) = 30.04$; time of day, $F(3, 273) = 3.51$].

TABLE 2. Number of insects in each group observed being fed by adult Yellow Warblers to young in three brood sizes at two ages.

	Brood size and age											
	3 YY		4 YY		5 YY		3 OY		4 OY		5 OY	
Insect group	♀♀ (48)[a]	♂♂ (91)	♀♀ (52)	♂♂ (83)	♀♀ (32)	♂♂ (111)	♀♀ (108)	♂♂ (121)	♀♀ (82)	♂♂ (159)	♀♀ (178)	♂♂ (134)
Chironomids and culicids (I)	22	28	26	29	1	34	68	110	117	247	95	73
Geometrid larvae (II)	8	48	15	42	18	91	10	37	6	17	34	49
Other larvae (III)	1	2	0	0	0	2	2	8	1	2	1	3
Other Diptera (IV)	1	0	1	1	3	5	5	1	5	1	0	1
All other insects (V)	1	0	1	1	0	5	5	6	13	51	15	5
Feeding trips with unidentified prey	19	16	15	21	10	7	42	43	21	42	55	44

[a] Total number of feeding trips observed.

Females fed broods of four 8-day-old young the largest number of items per trip (Table 1) and did not vary their rate with time of day [two-way ANOVA: brood size, $F(2, 238) = 25.91$; time of day, $F(2, 238) = 1.74$].

Males fed 2-day-old young more often than females regardless of brood size [ANOVA: broods of 3, $F(1, 94) = 8.54$; broods of 4, $F(1, 62) = 7.97$; broods of 5, $F(1, 70) = 29.95$]. With 8-day-old young, males and females fed broods of 4 at equivalent rates [$F(1, 62) = 0.68$], males fed broods of 3 more often than their mates did [$F(1, 60) = 14.3$], and females fed broods of 5 more often than males did [$F(1, 62) = 5.33$]. Both sexes fed 8-day-old young more often than 2-day-old young [females—broods of 3, $F(1, 78) = 61.9$; broods of 4, $F(1, 61) = 5.04$; broods of 5, $F(1, 66) = 69.0$; males—broods of 3: $F(1, 78) = 15.6$; broods of 4, $F(1, 61) = 22.3$; broods of 5, $F(1, 66) = 6.9$].

Males with 5 young brought a larger food load per trip than did females at both ages of nestlings studied. No other significant differences between parents were observed [ANOVA: 3YY, $F(1, 102) = 0.63$; 4YY, $F(1, 97) = 1.02$; 5YY, $F(1, 124) = 5.39$; 3OY, $F(1, 142) = 0.68$; 4OY, $F(1, 176) = 3.40$; 5OY, $F(1, 211) = 10.3$].

All parents except females with 5 young brought greater load sizes when feeding older young [females—broods of 3, $F(1, 93) = 8.27$; broods of 4, $F(1, 96) = 17.09$; broods of 5, $F(1, 143) = 3.52$; males—broods of 3, $F(1, 151) = 53.1$; broods of 4, $F(1, 177) = 52.5$; broods of 5, $F(1, 192) = 7.94$].

When the young were 2 days old, more food items were brought by males than by females. Overall, 2-day-old broods of 4 were fed more food items than broods of 5 or 3. When the young were 8 days old, more food items were brought by males to broods of 3 and 4 than by females, while the reverse was true for broods of 5. Overall, broods of 4 were fed more items than broods of 3 or 5 at this age.

Food items available and used.—As time of day did not affect the type of prey the adults brought to the young (Chi-square, $P > 0.05$ in 10 of the 12 cases), the observations from all time periods were combined. At each age, significant differences in the proportion of each of the five insect groups in the diet brought by females were observed among brood sizes (Table 2; YY: $\chi^2 = 30.6$, 8 df; OY: $\chi^2 = 36.3$). At both ages, females with 5 young brought more geometrid larvae and fewer chironomids and culicids than did females with broods of 3 and 4 young. There were also significant differences between 2- and 8-day-old young in the proportion of items brought by females with broods of 4 and 5 young (broods of 3: $\chi^2 = 4.2$, 4 df; broods of 4: $\chi^2 = 29.9$, broods of 5: $\chi^2 = 38.1$). A larger proportion of chironomids and culicids and a smaller proportion of geometrid larvae were fed to the older young in broods of 4 and 5, but females that were feeding broods of 3 maintained a relatively constant diet between the two ages.

The proportion of insects in each group observed being fed by males (Table 2) differed significantly among brood sizes at each age

TABLE 3. Total number of insects in each group found in the stomachs of nine 8-day-old warbler nestlings in each brood size.

Insect groups[a]	Brood size 3	4	5
I	76	109	71
II	28	17	21
III	2	4	4
IV	14	5	10
V	13	15	16

[a] See Table 2.

(YY: $\chi^2 = 20.5$, 8 df; OY: $\chi^2 = 103.4$). Again, broods of 3 and 4 were fed more chironomids and culicids and fewer larvae than broods of 5. The proportion of items in each group brought by males also differed significantly between the two ages (broods of 3: $\chi^2 = 34.3$, 4 df; broods of 4: $\chi^2 = 130.5$; broods of 5: $\chi^2 = 30.3$) and followed a trend similar to that of the females.

Intersexual differences in the proportion of items observed being fed to the nestlings were also significant, except between parents feeding four 2-day-old young (3YY: $\chi^2 = 12.7$; 4YY: $\chi^2 = 5.5$; 5YY: $\chi^2 = 10.3$; 3OY: $\chi^2 = 13.7$; 4OY: $\chi^2 = 10.8$; 5OY: $\chi^2 = 11.2$; all have 4 df). Males generally brought more geometrid larvae than did females. Females brought more chironomids and culicids.

The proportions of items observed being fed to nestlings and those in the stomachs (Table 3) differed significantly in each brood size, mainly due to differences in the proportion of insects in groups IV and V. These insects were usually small and were underestimated in the field. The stomach contents of the young in the three brood sizes were not significantly different ($\chi^2 = 13.5$, 8 df), although the trend found is similar to the field-observed diet in that the largest proportion of chironomids and the smallest proportion of larvae were fed to broods of four.

The prey items fed are compared in Figs. 1 and 2 to prey items available in each sampling period. Although the total number of insects varies, the relative importance of each group remained fairly constant throughout the observation periods. A Wilcoxon sign test was used to compare the proportion available in each group to the proportion (by number) of that group observed to have been fed. Adult Yellow Warblers selected geometrid larvae ($P = 0.016$) and avoided feeding all other larvae ($P = 0.031$) and all other insects ($P = 0.016$) when feeding 2-day-old young. Adults feeding 8-day-old young selected chironomids and culicids ($P = 0.008$), geometrid larvae ($P = 0.008$), and other larvae ($P = 0.063$) and avoided all other Diptera ($P = 0.016$) and all other insects ($P = 0.008$). Thus, adult Yellow Warblers selected particular prey items as food for their nestlings.

Weight and protein content of nestling food.—The average dry weights of insects in groups I, II, and III were 3.1, 6.0, and 8.5 mg, respectively (Biermann 1980). The weight of an "average" insect fed to a nestling was calculated for each parent with each brood size at each age by multiplying the number of individual prey items of each group being fed (Table 2) by the average weight of insects in that group, summing for groups I, II, and III and dividing by the total number of insects in the three groups. This estimate, multiplied by the total number of insects brought per half hour (Table 1) yields an estimate of the average weight of food items brought per half hour (see Table 4). Because the items observed being fed were biased toward larger prey, the true weight of food brought per half hour was smaller. As the number of feeding trips in which prey were unidentified was relatively constant (usually about one-quarter to one-third of the feeding trips, Table 2), however, the values calculated are useful in comparing the feeding rates.

Generally, males brought heavier prey items than did females. Heavier items were brought to 2-day-old young than to 8-day-old young, because a larger proportion of the diet of 2-day-old young was Lepidoptera larvae. Males feeding 2-day-old young brought more food to larger broods. Females fed 2-day-old young at a rate unrelated to brood size. Females brought more food to larger broods of 8-day-old young than to smaller broods. Males did not. Overall, at 8 days, broods of 4 were fed more food by weight than were broods of 5 or 3.

Other factors apparently are also important. The fat, ash, protein, and water content of insects, as well as their digestibility, may affect the proportion of the dry weight that is usable by the nestling. The proportion of dry weight that is protein was 59.8% and 62.6% for the chironomids and larvae, respectively. Protein content is likely to be the most important com-

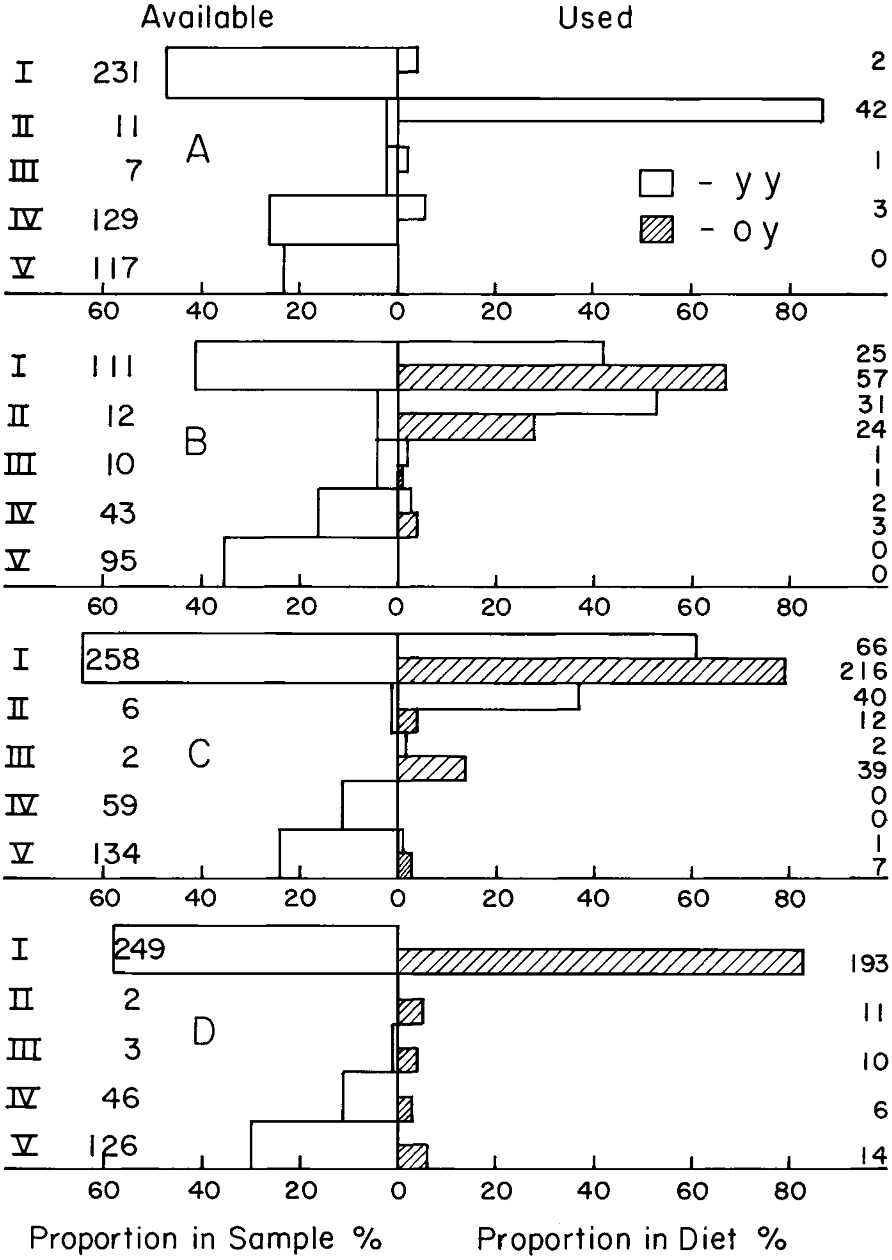

Fig. 1. Proportion, by number, of insects in groups I–V in sweep net samples, and the proportion of insects in each group observed being fed to 2- and 8-day-old Yellow Warblers in 1978. A, 12–16 June; B, 17–22 June; C, 23–27 June; D, 28 June–1 July. Absolute numbers of insects are given on the sides.

ponent of a nestling's diet, because rapid body growth occurs during this stage of development (Kear 1972).

The average dry weight of the insects was multiplied by the proportion of the weight that is protein to determine the amount of protein in the insects. The total weight of protein fed by the parents of the nestlings at each age and in each brood size was determined using calculations described above (Table 4). Compar-

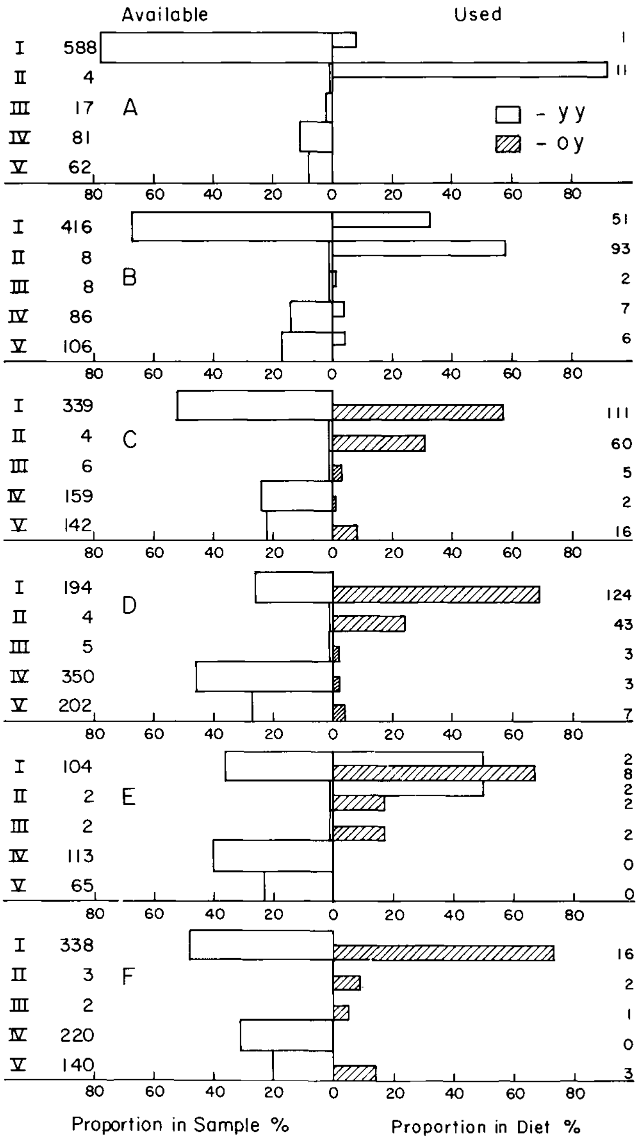

Fig. 2. Proportion, by number, of insects in groups I–V in sweep net samples, and the proportion of insects in each group observed being fed to 2- and 8-day-old Yellow Warblers in 1979. A, 20–24 June; B, 25–29 June; C, 30 June–4 July; D, 5–9 July; E, 10–14 July; F, 15–19 July. Absolute numbers of insects are given on the sides.

isons among brood sizes are similar to those described for the dry weight of food brought by the parents, but the differences in the amount fed among the brood sizes are generally decreased.

Growth rates.—As broods of 3, 4, and 5 young are fed different proportions of food items at different rates on a per nestling basis, these differences might be expected to affect the growth rates of the young. Fig. 3 shows the growth rate, measured as change in body weight, of nestlings in broods of 3, 4, and 5. Because the same nestlings were not weighed every day and the weights shown are means of all nestlings weighed, the curves do not conform exactly in shape to standard growth curves. The overall growth rates of young in the brood sizes can be compared using the

TABLE 4. Average dry weight (mg) and protein content (mg) of insects fed by male and female parent Yellow Warblers to broods of 3, 4, and 5 young at two ages.

Brood size and age	Average dry weight of average insect brought		Average dry weight of food brought per half-hour		Mean dry weight of protein per average item		Average dry weight of protein brought per half-hour	
	Males	Females	Males	Females	Males	Females	Males	Females
3 YY	5.0	4.0	11.6	4.8	3.2	2.5	7.4	3.0
4 YY	4.8	4.2	16.4	7.9	3.0	2.2	10.2	4.2
5 YY	5.3	5.9	19.5	5.3	3.3	3.7	12.2	3.3
3 OY	4.3	3.6	30.8	18.4	2.5	2.2	18.0	11.2
4 OY	3.3	3.3	45.8	19.4	2.0	2.0	27.0	11.8
5 OY	4.4	3.9	27.5	26.1	2.7	2.4	17.0	16.1

regression equations provided in Fig. 3. A test for the equality of slopes (Sokal and Rohlf 1969) showed no significant difference in the growth rate of the young in the three brood sizes [ANOVA: $F(2, 11) = 0.65$]. Using a graphical technique to convert the growth curve to a straight line (Ricklefs 1967), we calculated the specific growth rate constant (K) for young in each brood size, using a weight asymptote of 11.0 g. The rate constants (0.546, 0.551, and 0.541 for broods of 3, 4, and 5 young, respectively) again suggested similar growth rates of young in the three brood sizes.

DISCUSSION

FEEDING RATES AND FOOD LOADS

Time of day.—Time of day did not usually affect the feeding rate and load size of adult Yellow Warblers feeding their young. In many species, most feeding usually occurs just after dawn and at dusk, and the least occurs at midday or mid-afternoon (Best 1977, Nolan 1978, Pinkowski 1978). These variations are usually related to differences in the activities of the prey species, as many insects are most active in the coolest parts of the day, or are associated with the need of the birds to feed heavily just before and after the overnight fast. The diet of some bird species may also vary with time of day (Walsh 1978). In the present study, however, early-morning sampling was not done just after dawn, nor was evening sampling done just before sunset. The lack of dietary variation during the day indicates that insect activities did not greatly affect the foraging success of the birds.

Brood size and age.—Generally, adult feeding rate increases with an increase in brood size (Moreau 1947, Lack and Silva 1949, Lack and Lack 1951, Royama 1966, Morehouse and Brewer 1968, Hussell 1972, Best 1977, Walsh 1978). The feeding rate of adult Yellow Warblers was greatest in the largest brood size when broods were 8 days old. Food loads, however, were not the largest (Table 1). At 2 days of age, both feeding rate and food-load size were greatest for broods of 4.

Other workers have also found that feeding rate is not directly related to brood size. Pinkowski (1978) found no positive relation between brood size and feeding rate by either male or female Eastern Bluebirds (*Sialia sialis*). Seel (1969) found that the feeding rates for broods of 3, 4, and 5 House Sparrows (*Passer domesticus*) did not differ significantly.

Feeding rates were shown in our study and by several others to increase as the nestlings grew older (Gibb and Betts 1963, Royama 1966, Seel 1969, Nolan 1978, Pinkowski 1978, Walsh 1978). Larger young generally require more food to supply sufficient energy for thermoregulation and developmental processes.

The role of males relative to females in feeding the young varies among species. Nolan (1978) found that female Prairie Warblers (*D. discolor*) assumed a slightly larger proportion of the feeding duties, whereas Field Sparrows (*Spizella pusilla*) share this duty nearly equally (Best 1977). On our study area, male Yellow Warblers usually assumed the larger proportion of feeding duties.

Gibb and Betts (1963), Royama (1966), and Morehouse and Brewer (1968) noted that the feeding rate and the size of items brought were inversely related. Nolan (1978) found that adult Prairie Warblers brought similar sized food items, but, as the young grew older, both the

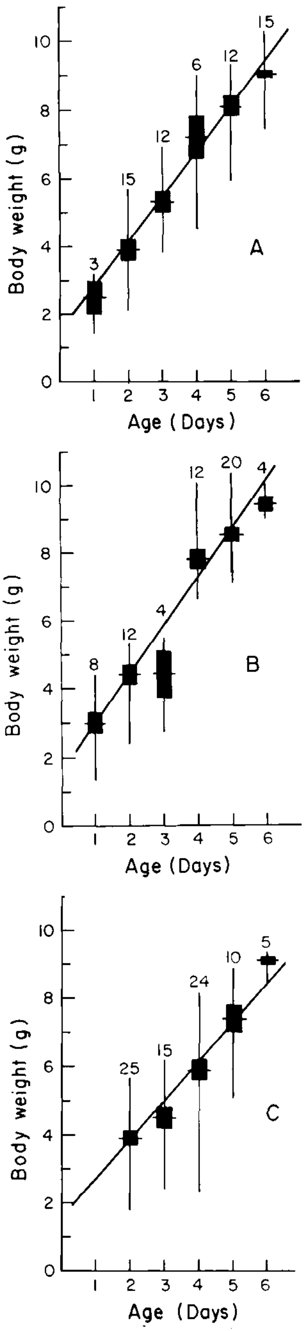

Fig. 3. Growth curves of Yellow Warblers in broods of 3 (A), 4 (B) and 5 (C) young. The horizontal lines are the mean weights, the vertical lines the ranges, and the solid bars denote 1 SE on each side of the mean. The numbers above each vertical line are sample sizes. Regression equations: 3 young, $y = 1.38 + 1.31x$; 4 young, $y = 1.56 + 1.39x$; 5 young, $y = 1.30 + 1.20x$. The slopes of all regression equations are significantly different from zero.

feeding rate and the size of items fed increased. Thus, he observed no inverse correlation between feeding rate and the size of items fed. In the Yellow Warbler, males brought heavier items and fed the young more often. Within each sex, however, the inverse relation between feeding rate and food size held.

DIET OF NESTLINGS

Busby and Sealy (1979) found the diet of adult Yellow Warblers during the breeding season at Delta to be composed mainly of Diptera, particularly chironomids. Studies of the diet of adult Yellow Warblers in other areas have found Hymenoptera or Homoptera and Coleoptera to be the major components of the diet (Kendeigh 1947, Frydendall 1967). Adult Yellow Warblers apparently are flexible in their choice of food and forage opportunistically (Busby and Sealy 1979).

Adult chironomids and culicids and larval geometrids were the main components of the diet of nestling Yellow Warblers. The proportion of these items in the diet changed with the nestlings' age. Two-day-old young were fed more geometrid larvae than were 8-day-old young, with a corresponding change in the proportion of chironomids and culicids. Stomach analyses confirmed, to an extent, feeding observations and indicated that chironomids, not culicids, were the most important insect in group I. Apparently, the abundant chironomids are an important source of nourishment for both adult and nestling Yellow Warblers during the breeding season at Delta.

Diet and prey availability.—Generally, adult Yellow Warblers did not feed their nestlings prey in proportion to its availability. They were selective. At both nestling ages, geometrid larvae were fed in proportions greater than were available. Other studies of passerine nestling feeding have found Lepidoptera larvae to be important components of the diet (Best 1977, Pinkowski 1978). In the present study, all other larvae and all other insects were under-represented in the diet of 2-day-old young, compared with what was available. When 2-day-old young were fed a geometrid larva, the parents often passed it back and forth between themselves and pulled on it, breaking it into smaller, more manageable pieces that were then fed to the nestlings. Attempts to feed a larva whole to the nestlings usually failed. Because other larvae are usually wider and heavier than geometrid larvae, they would have required even more processing by the parents before they could be fed to the young. Probably more effort is required than is practical. Best (1977) found that girth rather than length limited the size of food that young Field Sparrows could ingest. Several studies have shown that the size of food items increases with nestling age, suggesting that the relative size of the nestlings and the food may be important (Gibb and Betts 1963, Best 1977, Nolan 1978, Pinkowski 1978, Walsh 1978, Johnson et al. 1980). All other insects collected in the insect samples included many hard bodied insects such as Coleoptera, Hymenoptera, and Hemiptera, all of which may have been unsuitable food for young birds.

Chironomids and culicids and all other larvae were selected preferentially for 8-day-old young, as were geometrid larvae. At 8 days of age, the nestlings are nearly adult size and can swallow larger larvae whole. Chironomids and culicids have soft abdomens that are easily digested, and, because they move slowly, several can be brought to the nest in one trip. Part of the body, however, is enclosed in a chitinous exoskeleton that is less easily digested than soft-bodied insects (Borror et al. 1976). The extent of the occurrence of a gastric chitinolytic system in birds is unknown (see Jeuniaux 1961), but it has been found in most of the few species studied (Ziswiler and Farner 1972). It is probably reasonable to assume that not all of the protein of a hard-bodied insect is digestible by nestlings. Thus, the difference in the total digestible protein brought per half hour to broods of four and five 8-day-old young is probably smaller than the difference between the values calculated in Table 4.

The similarity in growth rates of the young in the three brood sizes (Fig. 3) indicates that differences in feeding rates and food items fed do not affect the growth of the young. Thus, the larger number of insects brought by parents with four young may have been of lower quality, as suggested, or, alternatively, the young in broods of four may have been overfed, in that they may not have been able to assimilate all the nutrients from their food. Overfeeding in birds has never been reported, however, and would be contrary to expectations of optimal parental behavior.

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SEASONAL VARIATION AND FUNCTION OF MOBBING AND RELATED ANTIPREDATOR BEHAVIORS OF THE AMERICAN ROBIN (*TURDUS MIGRATORIUS*)

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ABSTRACT.—American Robins (*Turdus migratorius*) displayed four classes of approach to a Screech Owl (*Otus asio*): silent approach, vocal approach, mobbing, and attacking. Mobbing and attacking were confined to the breeding season. Mobbing first appeared in March and reached a maximum duration per mobbing bird in May and a maximum frequency in June. Mobbing and attacking were most often performed by pairs of robins or by single birds. These responses were directed at a Screech Owl located on the territory of the pair or individual. Silent approach and vocal approach occurred at all times of the year. During the breeding season, birds approached a Screech Owl located on a territory other than their own, observed the owl being mobbed, but joined in mobbing only if the owl flew. Outside the breeding season, robins gathered in large mobile flocks. Birds in such flocks sometimes approached a Screech Owl but did not mob.

I suggest that the contexts in which these responses occurred indicate that mobbing and attacking are beneficial for robins only when birds are confined to territories or home ranges. The presence of young on territories further increases the amount of parental mobbing. *Received 20 August 1980, accepted 4 November 1981.*

MANY species of birds, in diverse orders, are known to exhibit mobbing behavior. The widespread occurrence of this behavior is somewhat surprising, for it often involves an animal seeking out a potentially dangerous predator and performing conspicuous displays near it. That mobbing may be risky is confirmed by reports of mobbing birds being captured by predators (Hartley 1950, Cade 1967, Denson 1979). As a result, the adaptive significance of mobbing has remained largely an enigma, although many hypotheses have been advanced (Marler 1956; Humphries and Driver 1967; Curio 1975, 1978; Cully and Ligon 1976).

Certain aspects of the behavior, however, do suggest possible functions. An association between the breeding season and an increased tendency to mob has been reported in a number of species (Bolles 1890, Altmann 1956, Curio 1975). In some cases actual possession of a nest is necessary for mobbing to occur (Horn 1968). This relationship between mobbing and reproduction indicates that mobbing may be a particularly advantageous response to predators during the breeding season, possibly even serving mainly as a nest-defense mechanism.

The objectives of this study were (1) to test for a breeding season-mobbing association in the American Robin (*Turdus migratorius*), and (2) to investigate the adaptive significance of this association, if it were found.

METHODS

From 1 June 1974 through 31 August 1976, field trials were performed on a regular weekly basis. The procedure during these trials was planned to simulate a natural mobbing episode. A mounted Screech Owl (*Otus asio*) was placed in a conspicuous location 2 m from the ground. A recorded Screech Owl call was then played by means of a cassette tape recorder with the speaker located 10 cm from the mounted specimen. The taped calls were played on either a Norelco Tape Cassette Carry-Corder "150" (Model E13302P) or a Panasonic AC/Battery Portable Cassette Recorder RQ-209AS. All trials were observed from concealed positions 10 m from the mount.

Comparative tests showed no significant difference between the response to a stuffed specimen and taped call and the response to a captive live owl and taped call. Observations of birds mobbing wild owls further confirmed the adequacy of the test situation. Using a similar experimental design, Curio (1975) found no difference between the response directed at stuffed specimens and live predators.

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TABLE 1. Percentage of successful trials, average minutes of mobbing/bird (AMM/B), and average number of birds/successful trial for each month (Ithaca, New York). Robins were present on study sites in significant numbers from 1 March through 15 November; a few individuals were present throughout the winter.

Month	Total trials	Successful trials	Total birds	Percentage of successful trials	AMM/B	Average number of birds/successful trial
January	35	0	0	0.0	0.0	0.0
February	18	0	0	0.0	0.0	0.0
March	37	2	3	5.4	1.0	1.5
April	59	7	11	11.9	3.2	1.6
May	103	24	36	23.3	5.9	1.5
June	134	44	67	32.8	5.0	1.5
July	151	36	65	23.8	4.1	1.8
August	172	15	15	8.7	2.7	1.0
September	91	0	0	0.0	0.0	0.0
October	95	0	0	0.0	0.0	0.0
November	54	0	0	0.0	0.0	0.0
December	29	0	0	0.0	0.0	0.0

Data for many variables were collected during each trial; variables that proved useful include the number of individuals mobbing, the presence or absence of vocalizations and displays, the number of attacks on the predator mount, and the total minutes of mobbing performed by each bird.

Data from the study period were totaled and then treated as a single 12-month series. For each month, the average number of minutes of mobbing per bird (AMM/B) was calculated by summing the minutes of mobbing and dividing by the total number of mobbing birds. Also calculated for each month were the percentage of successful trials (trials that resulted in mobbing) and the average number of mobbing birds per successful trial.

Means for each month were tested for statistical probability of equality using a single classification ANOVA, with means weighted according to the reciprocal of the variance of the samples from which they were drawn. This adjustment results in an approximate test of equality of means when variances are heterogeneous (Snedecor 1956, Sokal and Rohlf 1969).

The fieldwork for this research was carried out in the vicinity of Ithaca, New York. During December and January 1976, trials were also performed at various locations in Florida. The New York study sites consisted mostly of deciduous woodland where beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) predominate. Floodplains dominated by *Fraxinus* species and large areas of old field habitat were also sampled. Robins were common in all of these areas from early March until late October, with breeding densities averaging 5–8 pairs/ha.

Testing in Florida was done at Merritt Island National Wildlife Refuge and on Sanibel Island. Both areas contained extensive regions of coastal palmetto (*Sabal palmetto*) thickets. Robins were abundant in both localities, drawn in part by the fruiting palmetto. Where flocks were present, densities exceeded 1,000 birds/ha. Screech Owls were found at both Florida study sites.

Mobbing behavior is only one phase in a continuum of behavioral responses to a predator that range from fleeing to attacking (Simmons 1952). Although responses intergrade continuously, it is useful to categorize them for purposes of data collection. In this study positive responses (i.e. responses involving movement toward the predator) were divided into four classes:

Silent approach.—In many trials in which either the mounted owl or a captive owl was used, birds were observed locating the owl and then silently observing it for several minutes without vocalizing. Eventually, these birds flew off, usually leaving the vicinity of the owl.

Vocal approach.—Birds vocally approaching a predator gave alarm calls typical of mobbing birds but remained several meters away and exhibited few, if any, of the visual displays typical of mobbing. Such birds seemed to experience little risk of capture.

Mobbing.—Mobbing birds approached a predator closely (within 1 m) and performed a combination of visual displays and vocalizations. Visual displays typical of mobbing consist of intention movements to approach or flee, such as wing-flicking, tail-wagging, and nervous hopping. Mobbing vocalizations are loud and high-pitched. Generally calls are of 0.1 s or less in duration and of a narrow range of frequencies; this combination presumably makes the calls easy to locate (Marler 1959). Both visual displays and vocalizations are frequently repeated during mobbing.

Attacking.—Mobbing birds sometimes suddenly

TABLE 2. Attacks by Robins at study sites in Ithaca, New York. Attacks occurred only from April through August.

Month	Total trials	Trials with attacks	Total attacks	Average number of attacks/trials with attacks
April	59	3	5	1.7
May	103	6	81	13.5
June	134	7	14	2.0
July	151	5	8	1.6
August	172	6	12	2.0

ceased mobbing and pressed an attack directly on the predator. Such attacks consisted of short dashing flights, culminating in strikes on the predator, usually about the head or neck.

RESULTS

Robins were present in Ithaca in significant numbers from early March until middle November (with isolated individuals lingering through the winter), but mobbing was confined to the sampling period extending from March through August (with a single exception noted below). Monthly averages for the AMM/B index rose during this time from a minimum of 1.0 min of mobbing/bird in March to a maximum of 5.9 in May and then declined to 2.7 in August ($P < 0.05$, $F = 14.759$). The average amount of mobbing performed by each bird increased with the advance of the breeding season until May and then declined (Table 1).

The percentage of trials that was successful in producing mobbing among robins rose from a low of 5.4% in March to a peak in June of 32.8%. The percentage then declined to 8.7% in August (Table 1).

During the 6 months in which mobbing was observed, there was no significant change in the number of birds responding during each successful trial (Table 1). Trials in July averaged 1.8 birds/successful trial for a maximum, while in August a minimum of 1.0 was reached ($P < 0.05$, $F = 0.439$).

TABLE 3. Average number of Robins/trial displaying silent or vocal approach (SVA/ST) for each month. Total trials: TT; trials with silent or vocal approach: ST.

	Adult-plumaged birds			Immature-plumaged birds	
Month	TT	ST	SVA/ST	ST	SVA/ST
New York					
January	35	0	0.0	—	—
February	18	0	0.0	—	—
March	37	7	2.9	—	—
April	59	12	1.8	—	—
May	103	17	1.5	—	—
June	134	18	1.9	2	1.0
July	151	32	3.1	35	3.5
August	172	40	3.4	45	8.0
September	91	12	3.6	12	5.3
October	95	24	8.3	—	—
November	54	1	1.0	—	—
December	29	0	0.0	—	—
Florida					
December	57	15	17.9	—	—
January	35	11	35.2	—	—

Other responses that were closely related to mobbing also varied seasonally. Robins were observed attacking the owl mount only during the breeding season (Table 2). The number of attacks was highest in May. Attacks were incorporated into the general mobbing activities of the birds and consisted of swooping flights toward the mounted owl (usually directly at the head), followed by an abrupt retreat. Only one attack was observed that was not preceded by preliminary displays of mobbing. Robins mobbing wild owls attacked them in a similar fashion.

The behaviors of silent and vocal approach were more common in Ithaca outside the breeding season (Table 3). At the Florida study sites, large numbers of robins were exposed to the owl mount and taped call. None of these birds was observed to mob, although some displayed silent or vocal approach.

Silent approach was typical of immature robins, which were first observed responding in June (Table 3). These birds always arrived after adult birds were mobbing and may have been attracted by the adults' alarm calls rather than by the owl call. By July many immatures were attracted, and most continued to display silent approach. In August the number of immature robins attracted outnumbered adults. At this time immatures responded directly to the owl call and displayed vocal approach. Immature robins were observed to mob on only two occasions (22 July 1974, 11 August 1976).

DISCUSSION

Seasonal variation in mobbing.—Several studies of mobbing behavior have noted an association between this behavior and reproductive activity (Edwards et al. 1949, Root 1969, Curio 1975). In the present study, a peak in mobbing activity occurred in May and June (Table 1), markedly overlapping with the interval of 2 May through 23 June when 70% of the hatching and fledging of young could be expected (Howell 1942). The willingness of robins to mob during the breeding season probably stems from at least two factors: (1) birds are territorial at this time and lack the option of easy relocation away from predators on their territories, and (2) birds are likely to have eggs or young on their territories.

Restriction to a small home range or territory may be an important factor influencing the performance of mobbing. The single instance of postreproductive mobbing by robins observed in this study occurred on one of the New York study sites in January. Two robins, confined to a sumac (*Rhus typhina*) thicket by heavy snows, mobbed vigorously when exposed to the mounted owl and taped call. This was in marked contrast to the response typical of robins outside the breeding season (see below).

The relationship between mobbing and territoriality is further demonstrated by a consideration of Table 1, which indicates that, although the percentage of trials successful in stimulating mobbing increased greatly from March until June, the number of birds mobbing during a successful trial did not vary significantly during this period, always being less than an average of two birds. The territorial distribution of the mobbing birds made it apparent that they were individuals maintaining territories where the Screech Owl was located.

Just as maintenance of a territory seems to have the effect of increasing the intensity of mobbing, a breeding bird's genetic investment in young is likely to have a similar effect. The risk entailed by a mobbing bird would be counterbalanced by an increase in fitness through kin selection if mobbing reduced mortality in that bird's young. If this were true, mobbing intensity would increase as the egg-nest unit grew older and parental investment increased. This was observed to occur by Howell (1942) and is suggested by the AMM/B index (Table 1). Mobbing seems to follow a pattern of development during the breeding season similar to that observed in antipredator behaviors such as distraction displays and reactivity to distress calls (Stefanski and Falls 1972, Barash 1975).

The manner in which mobbing may function to reduce predation remains open to debate. Because mobbing by robins is sometimes interspersed with direct attacks on the predator (Table 2), and because mobbing displays are often virtually identical to displays used during territorial encounters with conspecifics, it is likely that mobbing functions in this species to drive predators away. Certainly the advantage inherent in driving a Screech Owl away from a territory is evident from a consideration of the owl's diet, which during the spring may consist predominately of small and medium-sized birds (Allen 1924, Stewart 1969, Van Camp and Henny 1975).

Silent and vocal approaches.—Silent and vocal approaches seem to occur in situations in which the risk of mobbing is greater than any benefits that might result. Silent approach is a low-risk behavior allowing birds to locate and then avoid a predator. Vocal approach may discourage a predator from further hunting without the risk of the close approach necessary for mobbing (see "Perception Advertisement" *in* Curio 1978).

Silent and vocal approaches appear in two contexts: (1) Breeding birds show these responses when locating predators not on their own territories. Observations of the mobbing of live owls revealed that birds from distant territories were often attracted to a mobbing pair but joined in mobbing only if the owl was forced into flight by the mobbers. A similar observation has been made of colonially nesting gulls by Kruuk (1976). (2) Birds show these responses when they abandon territories at the close of the breeding season. All of the birds attracted to the mounted owl and taped call from September until November in New York were such birds (with the single exception of the mobbing pair noted above). Similar responses were obtained in Florida during December and January. The factor most responsible for the cessation of mobbing at the end of the breeding season and the substitution of silent or vocal approaches appears to be the movement of territorial birds into highly mobile nonbreeding flocks. Robins in such flocks would seem to have little to gain by mobbing; it is presumably more adaptive for them to locate a predator and then avoid further contact with it.

The numerous theories currently being proposed as to the function of mobbing have been synthesized by Curio (1978) into nine hypotheses with resultant predictions of prey and predator behavior. Of these hypotheses, some variation of Curio's "Moving on" model seems most consistent with my results. Other factors, however, may be operating concurrently. For example, Curio et al. (1978) suggest the possibility of cultural transmission of information about predators. Such an hypothesis is supported by observations in this study indicating that immature robins respond initially to calls of mobbing adults and closely observe these adults. Because many factors may be operating to cause mobbing, it is useful to keep in mind that many of the proposed hypotheses are not mutually exclusive. Also, given the frequent occurrence of mobbing among groups of unrelated birds (and mammals), it would be unrealistic to hope for an explanation of the function of mobbing that would apply to all species in all situations.

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EGG PREDATION BY NORTHWESTERN CROWS: ITS ASSOCIATION WITH HUMAN AND BALD EAGLE ACTIVITY

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ABSTRACT.—Predation by Northwestern Crows (*Corvus caurinus*) on the eggs of Double-crested Cormorants (*Phalacrocorax auritus*), Pelagic Cormorants (*P. pelagicus*), Glaucous-winged Gulls (*Larus glaucescens*), and Pigeon Guillemots (*Cepphus columba*) was studied in the summers of 1976–1980. Crows took eggs to specific sites on their territories where they ate them and where we counted the shells. In 1980, the crows took 1,167 cormorant eggs, an estimated 22% of all eggs in first clutches. When Bald Eagles (*Haliaeetus leucocephalus*) were present, more cormorant eggs were lost to crows than on days when eagles were absent. More eagles were present on weekends than on weekdays, presumably because the local eagle population was kept inadvertently on the move by people seeking recreation on the water. *Received 10 November 1980, accepted 1 September 1981.*

CROWS (*Corvus* spp.) are notorious predators on the eggs and young of other birds. This paper documents the predation of an island population of Northwestern Crows (*Corvus caurinus*) on the eggs of Double-crested Cormorants (*Phalacrocorax auritus*), Pelagic Cormorants (*P. pelagicus*), Glaucous-winged Gulls (*Larus glaucescens*), and Pigeon Guillemots (*Cepphus columba*). The study was conducted on Mandarte Island (48°38′N, 123°17′W), British Columbia. The cliffs on the southwest side of the island rise abruptly to a height of 10–30 m, and the island slopes downward to a height of 1–5 m along the northeast shore (Fig. 1). Pelagic Cormorants nest singly or in small, scattered groups on rocky ledges along the steep cliffs, while Double-crested Cormorants nest in tight colonies at the top of the cliffs. Gulls nest in the grass on either side of a strip of shrubs and trees that grow along the long, central axis of the island, and the guillemots nest in burrows under rocks and in crevices in the meadows and the cliffs, respectively. The crows nest in the shrubs and trees (Fig. 1).

METHODS

Starting about 1 h before sunset, my colleagues and I searched the island daily in May, June, and July 1978, 1979, 1980 and about three times per week in 1976 and 1977 for seabird eggs that had been preyed upon. In most cases we had no difficulty in deciding how many whole eggs were represented by the partial shells and fragments found. When in doubt, we guessed conservatively. We removed all the eggshells and shell fragments and either cached them in places to which the crows had no access (1976–1979) or took them away in a plastic bag (1980). The crow territory on which the eggs were found was recorded. In 1978 and 1980 we distinguished between fresh eggs (taken on the day on which they were found) and old eggs (taken the previous day or earlier). We did not attempt to distinguish between the eggs of the two species of cormorant, because the eggs are similarly colored and shaped and overlap in size [Double-crested Cormorant: length 62.65 ± 1.85 mm, width 39.27 ± 1.16, $n = 44$ (Verbeek MS); Pelagic Cormorant: length 58.85 ± 3.83 mm, width 37.37 ± 1.23, $n = 20$ (Palmer 1976)], and many of the eggs were too fragmented to measure. The presence or absence of Bald Eagles was recorded daily in all 5 yr. In 1980 we also recorded how many times eagles flew over the island each day and whether or not they disturbed the gulls and the cormorants. The researchers on Mandarte Island carefully avoided disturbing the cormorants throughout this study.

RESULTS

Although the total number of cormorant eggs found varied among years, most were found in June each year (Table 1). Similarly, eggs of Glaucous-winged Gulls were found mostly in June (Table 2). The crows took few eggs of Pigeon Guillemots, presumably because their nests were concealed and difficult to enter. We may have misidentified some fragmented Pigeon Guillemot eggs as gull eggs.

A crow transports a whole cormorant egg in its bill (lengthwise) and takes it to a secluded spot on its territory to be stored or eaten (see also Montevecchi 1976). All storage sites were located within or at the outer edge of the

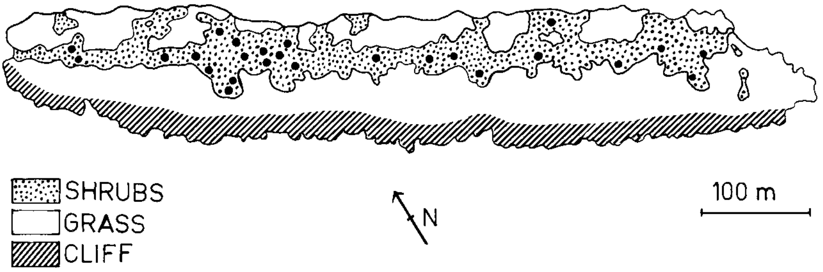

Fig. 1. Mandarte Island. The black dots represent the location of crow nests in 1980.

shrubs and trees. A pair of crows typically used the same site(s) throughout the season and usually the same sites were used each year. Sites were variable in nature, but all had some object that offered visual concealment from above. Eggs were hidden under a shrub, under a fallen tree trunk, among exposed tree roots, at the edge of small earth banks, under overhanging rocks, and inside an unused shed. The crows never took eggs to sites such as an open meadow where they would be in full view. A pair of crows thus could accumulate many eggs at the same site(s) in the course of a summer. It appeared that each pair of crows (and presumably each individual) had its own consistent way of opening an egg; some made a hole in the side of the egg and ate the contents through it; others fragmented the shell. Although some of the opened eggs contained some albumen when we found them, none contained yolk, and we rarely found cormorant eggs in advanced stages of incubation (blood inside the shell).

Cormorant eggs and young were taken from the nest by crows either during nest changeovers, when one incubating parent left the nest to be replaced by its partner (Drent et al. 1964, pers. obs.) or during disturbances when cormorants left their nests. Disturbances often occurred when adult Bald Eagles, which nested on neighboring islands, and other nonbreeding eagles visited Mandarte Island. Bald Eagles prey on the adult gulls (pers. obs.) and their chicks (Hayward et al. 1977, pers. obs.), and they have been reported to take Pelagic Cormorants as well (Campbell 1969).

At the arrival of a Bald Eagle, gulls were the first birds to respond. If the eagle flew low over the island, the gulls would fly up, and, as the eagle continued to approach the birds, a wave of anxiety spread down the length of the island. At the first indication of an approaching eagle, the crows appeared in the tops of bushes and trees. As the excitement increased, the crows flew high into the air, which is a typical, direct response of the genus *Corvus* to potentially dangerous avian predators. It gave them the direct advantage of being above the predator and the indirect advantage of an overview of the island. Within seconds, crows from all over the island converged on the cormorant cliffs, where they soared in updrafts over the nests, dropping down swiftly to take an egg or young when the opportunity arose. We have seen incubating, female crows leave their nests during such disturbances to take an egg quickly, eat it on the territory, and return to incubate. During some disturbances, such as on 28 May 1976, we saw a crow bring an egg to its usual hiding place, deposit it there, then head

Table 1. The number of cormorant eggs found in Northwestern Crow territories by month and year.

	1976		1977		1978		1979		1980	
Month	Number	%	Number	%	Number	%	Number	%	Number	%
May	102	35	33	12	154	37	139	10	207	18
June	170	58	203	76	176	43	827	60	533	46
July	22	7	31	12	82	20	422	30	427	37
Total	294		267		412		1,388		1,167	

Table 2. The number of Glaucous-winged Gull (GWG) and Pigeon Guillemot (PG) eggs found in Northwestern Crow territories in 1978, 1979, and 1980.[a]

	1978		1979		1980	
Time	GWG	PG	GWG	PG	GWG	PG
15–31 May	2	0	0	0	3	0
1–15 June	15	1	14	0	22	1
16–30 June	26	2	28	1	40	0
1–21 July	25	0	25	1	32	0

[a] Comparable data were not collected in 1976 and 1977.

Table 4. Frequency of freshly taken cormorant eggs found on weekends (Friday to Sunday) and weekdays (Monday to Thursday).[a]

	Weekends (3 days)		Weekdays (4 days)	
Year	Number of eggs	Percentage	Number of eggs	Percentage
1978	194[b]	56	152	44
1980	525	59	373	41

[a] Only in 1978 and 1980 did we distinguish daily between freshly taken cormorant eggs and those taken the previous day or earlier but not found by us.

[b] In both years significantly more cormorant eggs were taken by crows on weekends than on weekdays (Chi square test, $P < 0.001$).

back immediately to get another one. After a single prolonged eagle disturbance on 21 June 1980, we found 17 recently laid eggs on one crow territory. There is little doubt that the eggs were brought in by a pair of crows, one after the other and eaten later when the disturbance was over. Some uneaten eggs were cached. When such eggs were left by us, they were eaten invariably within the next 2 days.

Not all Bald Eagles that visited the island caused disturbances. Some merely flew over the island en route elsewhere. Eagles, especially immatures, would rest on the island occasionally. They typically did this in the few trees on the island, but sometimes they rested near the top of the bare cliffs where the Double-crested Cormorants nested. In the latter case, the cormorants left their nests and continued to fly back and forth along the cliffs until the eagles departed. During such disturbances, the crows had unhindered access to the cormorant nests. The number of days in each month on which eagles were present on the island over the 5 yr is shown in Table 3. In 1976, 1977, and 1978, the percentage of days in each month that eagles were present declined from April to July, but in 1979 and especially in 1980 eagles were present at about equal frequency throughout the season (Table 3). Visits of the eagles to the island were apparently more common during this study than they were in 1959 and 1960 (Drent et al. 1964).

Another source of disturbance was visits of small boats (sailing vessels, fishing boats, and sightseers) too close to the cormorant cliffs. In 1978 and 1980, when we distinguished daily between fresh eggs and old ones (see Methods), significantly more fresh eggs were found on weekends (including Fridays, as many small vessel operators appeared to start their weekends early) than on the remaining 4 days of the week (Table 4). The daily take of fresh cormorant eggs in 1980 is shown in Fig. 2. In addition, significantly more eagle scares also occurred on weekends than on weekdays, and many more cormorant eggs were taken on days with eagle scares than on days without scares, regardless of the time of the week (Table 5). In the absence of eagle scares, no significant differences existed between the number of eggs taken on weekends and on weekdays (Table 5).

The breeding populations of the two cor-

Table 3. The number of days people spent on Mandarte Island each month and the percentage of those days during which Bald Eagles were present.

	March		April		May		June		July	
Year	Days	%	Days	%	Days	%	Days	%	Days	%
1976	10	70	21	71	31	45	30	20	29	7
1977	4	75	19	75	31	55	30	47	29	41
1978	0	0	23	61	31	45	30	30	31	23
1979	6	67	29	62	31	65	30	70	22	23
1980	0	0	7	100	31	68	30	80	21	71

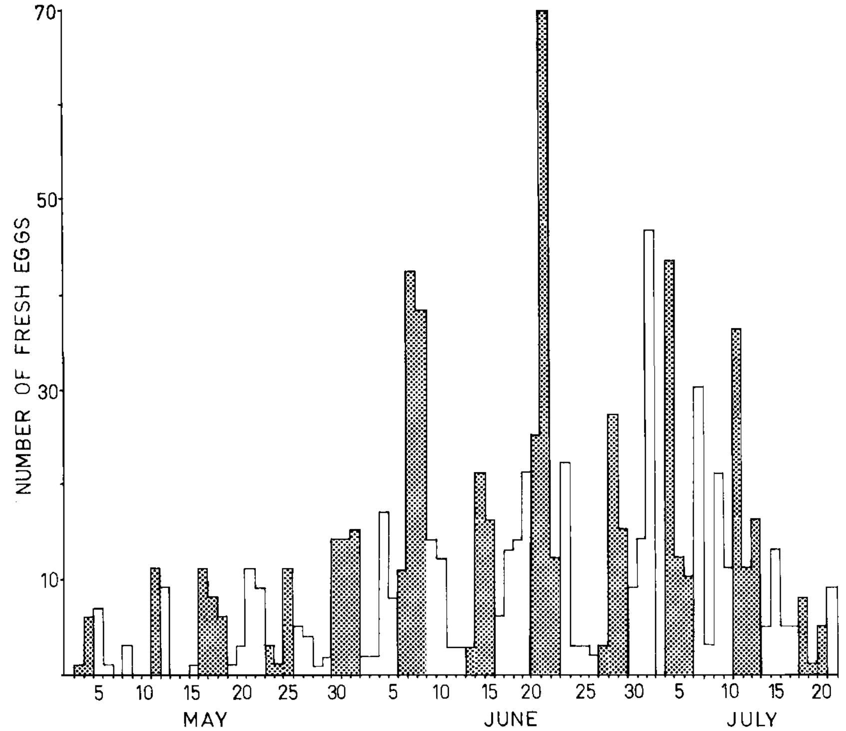

Fig. 2. The number of freshly taken cormorant eggs found in 1980. The shaded bars represent weekends and the unshaded bars represent weekdays as defined in Table 4.

morant species on Mandarte Island have increased since Drent et al. (1964) reported on them. In 1980 we counted 545 nests of Pelagic Cormorants and 794 nests of Double-crested Cormorants. These counts were made from a boat, and the count of Double-crested Cormorant nests may be an underestimate. The mean clutch size for Pelagic Cormorants (3.83 eggs, $n = 52$) does not differ significantly from that of Double-crested Cormorants (3.94, $n = 109$, Robertson 1971). Thus, the cormorants on Mandarte Island potentially could have laid 5,200 eggs in 1980 (not counting replacement clutches), of which the crows took 1,167, or

TABLE 5. Relationship between presence or absence of Bald Eagle scares, time of the week, and the number of freshly taken cormorant eggs found in 1980.

	Weekends[a]				Weekdays		
	Number of days	Number of scares	Eggs taken		Number of days	Number of scares	Eggs taken
With scares	23	68[b]	451[c]	With scares	24	46	270
Without scares[d]	13	0	74[e]	Without scares	22	0	103

[a] Weekends as defined in Table 4.

[b] Significantly more eagle scares occurred on weekends than on weekdays (Chi-square test, $P < 0.05$).

[c] Significantly more eggs were taken on weekends than on weekdays, (Chi-square test, $P < 0.001$), in the presence of eagle scares.

[d] Eagles absent all day or present but flew over high or otherwise did not disturb the cormorants.

[e] No significant difference exists between eggs taken on weekends and weekdays in the absence of eagle scares (Chi-square test, $P > 0.05$).

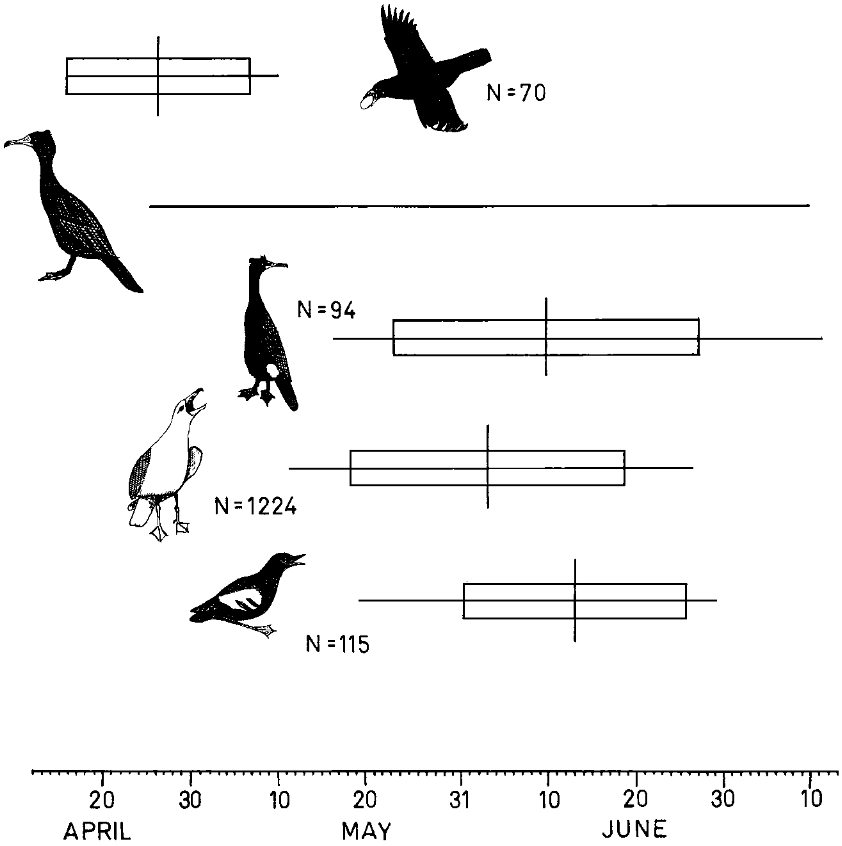

Fig. 3. The mean and standard deviation of clutch commencement of four avian species nesting on Mandarte Island. Only the range is shown for Double-crested Cormorants, because insufficient data were available. The data for cormorants and Pigeon Guillemots are based on Drent et al. (1964); those for crows and gulls are based on this study.

about 22%. About 2,200 pairs of Glaucous-winged Gulls nest on the island, the same as in 1962 (Vermeer 1963). The mean clutch size was 2.74 (n = 1,027, Verbeek MS). The crows took few of the eggs (Table 2). Drent et al. (1964) estimated the breeding population of Pigeon Guillemots at approximately 100 pairs, and they thought that the colony had reached maximum size. The mean clutch size was 1.91 (n = 162, Drent et al. 1964), so that a total of 191 eggs in first clutches was laid. The number of crows nesting on Mandarte Island increased from 13 pairs in 1976 to 25 pairs in 1980. Besides these breeding pairs, some nonbreeding yearlings (young of the previous year) were present, and some birds occasionally visited from neighboring islands. The number of yearlings and visitors was highest in April and early May. Probably not more than 5–10 yearlings and visitors were involved in 1980. The mean dates and ranges of egg laying of the crows and the other species are shown in Fig. 3. The first cormorant eggs taken by crows on Mandarte Island were found on 30 April 1977, 25 April 1978, 29 April 1979, and 28 April 1980.

Discussion

The Northwestern Crow on Mandarte Island nests early, well ahead of the seabirds whose eggs it eats (Fig. 3). We do not wish to imply, however, that early nesting in the crow has evolved in response to the nesting of the other species, because the Northwestern Crow nests early outside seabird colonies as well. Nevertheless, on Mandarte Island, the crow has cormorant eggs and those of other seabirds available to it from late April to late July (Fig. 3). The crow is mainly a predator of cormorant eggs, and I suspect mainly of Pelagic Cormorants. The Pelagic Cormorant nests tend to be isolated from one another, in contrast to those of Double-crested Cormorants, which nest in tight groups. The latter's colonies may be more difficult for a crow to enter, and perhaps the birds are less easily panicked. Additionally, Montevecchi (1976) has shown that crows prefer smaller eggs over larger ones. The apparent freshness of the eggs that were taken, even late in the season, suggests that perhaps a large proportion of the eggs were obtained from the same victims, which may have lost first as well as possible replacement clutches. It is possible that the cormorants flush easier from newly laid eggs than from those that have been incubated for some time.

Very few eggs of Pigeon Guillemots were taken (Table 2), as was shown also by Drent et al. (1964). Glaucous-winged Gulls also lost few eggs to Northwestern Crows. When an eagle caused the gulls to leave their nests temporarily, the crows on the island did not fly to the gull nests but to those of the cormorants. Gull eggs are not available otherwise, as the eggs are covered almost constantly. Most gull eggs that were taken by the crows were probably those that were abandoned after the others in the clutch had hatched. Table 2 shows that most of the gull eggs appeared on crow territories in the second half of June and into July, and we noticed that these eggs consistently smelled putrid, indicating that they had been spoiled for some time. I believe that most of the egg loss suffered by Glaucous-winged Gulls is due to intraspecific predation.

The increased predation of cormorant eggs in 1979 and 1980 (Table 1) is undoubtedly due in part to the increase in the crow population on the island, but more important, to the continued, frequent visits of eagles in June and July (Table 3). It is clearly shown in Table 5 that cormorants lose more eggs to crow predation on days with eagle scares than on days without eagle scares. In addition, more eggs are lost on weekends (Table 4, Fig. 2) than on weekdays (Table 5). It appears that the weekend activity of people seeking recreation on the water and along the shores of islands surrounding Mandarte Island inadvertently stirs up the eagle population. People, then, are directly (sailing too close to the cormorant colony) and indirectly (stirring up the eagles) responsible for part of the egg loss suffered by the cormorants to Northwestern Crows.

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TERRITORY SIZE IN *MEGACERYLE ALCYON* ALONG A STREAM HABITAT

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ABSTRACT.—Belted Kingfishers (*Megaceryle alcyon*) defend both breeding and nonbreeding territories. The small nonbreeding territories serve as feeding territories, and their size is inversely correlated to food abundance. In the breeding season, when nest sites are a limiting resource, territory size does not significantly correlate with food abundance. The average weight of fledglings/nest, however, is significantly correlated with territory size. In both seasons, kingfishers appear to use stream riffles as preferred foraging sites, although pools are more prevalent. Riffles may represent environmental cues by which individuals assess habitat quality. *Received 19 February 1981, accepted 30 September 1981.*

NUMEROUS studies have revealed correlations between territory size and various environmental parameters. Most frequently, resource density (Pitelka et al. 1955, Stenger 1958, Gill and Wolf 1975, Salomonson and Balda 1977) and/or population density (Myers et al. 1979, 1980; Ewald et al. 1980) are cited, but, as is now becoming evident, the proximate causal mechanisms responsible for these correlations are not always obvious. For example, although a negative correlation between territory size and food density may imply that an animal has the ability to assess resource density in relation to its needs, it may actually only reflect the increased population pressure in areas that attract many animals because of high food density. Alternatively, negative correlations might result from an animal's recognition of habitat factors that are directly associated with food (Hildén 1965, Morse 1976) rather than its assessment of food itself. Seastedt and Maclean (1979) have shown that the size of breeding territories of Lapland Longspurs (*Calcarius lapponicus*) is inversely related to the "expected" food density of the habitat comprised by the territory rather than to the actual food density in a given year. They conclude that longspurs respond to the habitat composition of an area rather than to the food density.

The relative importance of different environmental parameters as determinants of territory size may be dependent upon the type of territory defended [see Nice (1941) for classification of territories]. For example, breeding territories of birds usually possess multiple resources, such as nest sites and food, while non-breeding territories are often only "feeding territories" (Welty 1975); thus, in the breeding season, the number and distribution of available nest sites may influence the suitability of a habitat (von Haartman 1959). If nest-site limitations restrict the total number of breeding birds, territory sizes may become less dependent upon the availability of other resources such as food.

Belted Kingfishers (*Megaceryle alcyon*) are overtly aggressive birds that, along small streams, defend territories with well-defined boundaries and maintain exclusive use of the resources on their territories. Although the strong territorial nature of this bird is well known to naturalists, I am unaware of any previous empirical studies reporting analyses of the territoriality of this species. During the breeding season (March–June), both the male and female of a breeding pair jointly defend the territory on which their nest is located. Nest sites are chosen before the boundaries of breeding territories are firmly established (Davis 1980). In the autumn, birds of both sexes, including the young of the year, defend individual territories. The present study investigates possible determinants of territory size in the Belted Kingfisher in both the breeding and nonbreeding seasons.

STUDY AREA AND METHODS

Kingfishers were observed along a 16.8-km stretch of Indian Creek in rural southwestern Ohio. During

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the study period, Indian Creek had an average flow rate of 1.9 ± 0.4 m^3/s, although runoff produced from heavy rains occasionally increased the volume of flow (at times by as much as 10×). Creek width and depth varied from 5 to 19 m and 0.05 to 1.8 m, respectively, at normal flow. Turbidity was usually low except after heavy rains. Substrate varied; loose rock was predominant in riffles, while gravel and sand were the usual substrate of deeper pools. Nesting banks suitable to *M. alcyon* occur regularly along Indian Creek where the water erodes soil from bordering banks. Secondary forest growth dominates much of the creekline. Dominant tree species are American sycamore (*Plantanus occidentalis*), sand bar willow (*Salix interior*), several maple species (*Acer* spp.), and a variety of oaks (*Quercus* spp.).

The bulk of the data was collected between January 1978 and October 1979. Kingfishers were banded with U.S. Fish and Wildlife bands and marked with lead-free paint along the edge of the rectrices, using a combination of four colors. Individual birds could easily be identified in the field within a 50-m range using binoculars.

The territory size of marked individuals was measured as length (m) instead of as area, because territories followed the course of the stream. Territory sizes were assessed by recording the movement of marked individuals that were "herded" along their territories (Wiens 1969). By walking along the stream, I forced the resident kingfisher(s) to fly ahead until the end of the territory was reached. At this point the kingfisher(s) would reverse direction to fly back into its territory. The locations of the up- and downstream boundaries were determined a minimum of five times by this method. The site of aggressive confrontation between adjacent territory holders was used to confirm boundaries between territories. Lateral boundaries of territories were demarcated by the treeline along the edge of the stream. The following information was later transferred to detailed maps: length and width of stream, depth measurements of stream, lengths of pools and riffles, lengths of exposed banks, location of nests, and number of perches along the stream's borders. Riffles were defined as turbulent flow (5–15 cm in depth) connecting pools. Six nonbreeding territories were measured in the fall of 1978, 11 breeding territories in the spring of 1979, and 21 nonbreeding territories in the late summer and fall of 1979.

Two methods were used to determine the size and species of prey selected by *Megaceryle alcyon*. In the first (24 May–23 June), I assessed the species and size of prey brought to the nest by observing adult feeding activity with the aid of blinds and a 20× telescope. Because kingfishers carry prey in their beaks, I could estimate fish size by comparing the length of the fish with the bird's bill (culmen length of individual birds was recorded during banding; Drent 1965). Prey were classified to family, genus, or species by noting the morphological characteristics of the respective taxonomic groups. Cyprinids were classified into one of three groups: stonerollers (*Campostoma anomalum*); minnows, which included all identifiable cyprinid species other than *C. anomalum*, or unidentified cyprinids, which included all specimens that could not be identified to genus. The second method (1 June–23 June) involved placing velcro collars around the necks of nestling kingfishers for a period of 2 h from 0700 to 0900. This procedure prevented the young birds from swallowing food brought to them by the adults, and, as a result, fish accumulated at the entrance of the nest chamber. Weight, length, and species of these fish were recorded. Additional data on prey size and type were collected as kingfishers were observed fishing or when items were dropped into the mist net during banding of adults.

Estimates of food abundance were obtained for six nonbreeding territories (September–October 1978) and for six breeding territories (June 1979) by sampling the entire length of each territory by electroshocking. A shortage of manpower prevented fish sampling on any of the 21 nonbreeding territories measured in 1979, but in October 1979, 1,200 m of Indian Creek were electroshocked, with pools and riffles sampled separately, in order to document the relative location of the different fish species. Electroshocking was accomplished by suspending two electrodes, positioned at opposite ends of 1.3-m pole, in the water while moving upstream at a constant speed. Current was supplied to the electrodes by a 110-volt AC (1,500 watt) generator. Shocked fish were collected in nets by two persons following a third person carrying the electrodes. Fish collected were counted and classified according to size and species before they were returned to the stream. Fish mortality was reduced to less than 1% by supplying oxygen to the collecting buckets via air-stone and portable air pump.

Electroshocking was the method of choice for several reasons: (1) it was more practical for sampling long stretches of streams (seining was the alternative method); (2) sampling of only surface fish was desired; and (3) although small fish are generally less sensitive to sampling by this method than larger fish, the size of fish vulnerable to predation by kingfishers (4–14 cm) appears easily sampled by electroshocking (McCormack 1962; results of preliminary sampling by the author). Fish were assigned into five size classes: 4–5.9 cm, 6–7.9 cm, 8–9.9 cm, 10–11.9 cm, and 12–14 cm. Fish smaller than 4 cm and larger than 14 cm were excluded from the samples, as these extreme sizes were never seen taken by kingfishers.

For each fish species, 15 specimens in each size class were weighed to obtain an average weight for that size class. These averaged weights were multi-

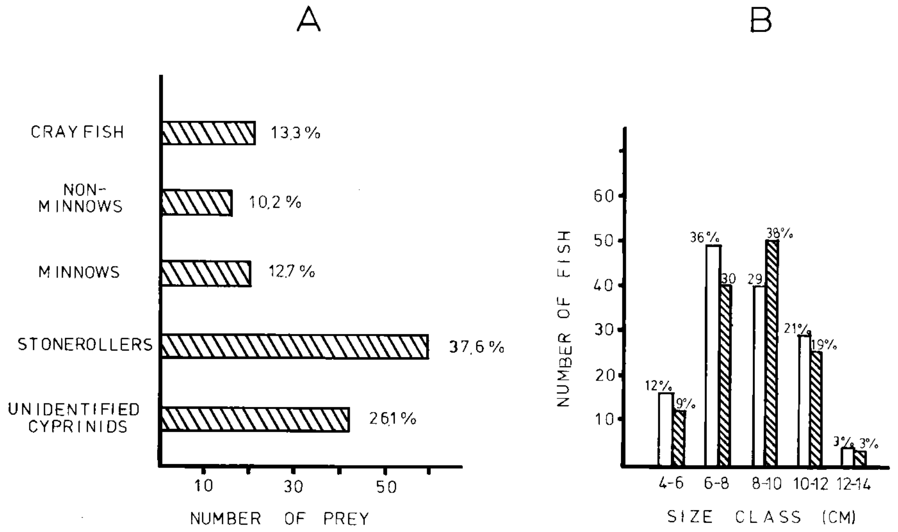

Fig. 1. Food capture data. Shown are the species composition (graph A) and size (graph B, hatched bars) of prey items taken by kingfishers. Data are from observations made on 22 dates and from velcro collar method (see text for details). Open bars in graph B represent the expected number of fish in each size class that should be taken by kingfishers, calculated from the percentage of each size class present in electroshocking data (breeding season 1979, total number of fish sampled = 3,678).

plied by the number of individuals sampled within each size class; then, all size classes were added together to obtain the total grams of fish per species. The number of grams of each species were added together and divided by the length of stream sampled to obtain the total grams per meter of stream. Relative food abundance per territory was calculated from these data (grams$\cdot$meter$^{-1}\cdot$territory^{-1}).

Preferred foraging sites of individual birds were identified. Each time a bird was observed foraging, selected stream parameters of the immediate habitat were recorded, e.g. whether the individual was seen fishing in a shallow pool (depth < 30 cm), a riffle (as previously defined), or deep pool (depth > 30 cm). Both sexes were included, and data were collected on 15 separate dates during the fall of 1979.

Between April and June 1979, data were collected from 14 nests on Indian Creek. Recorded were: (1) number of eggs laid, (2) number of eggs hatched, (3) weight of nestlings (g), (4) incubation period (days), and (5) number of young fledged. To sample each nest, I dug an entrance from the top of the bank down to the backside of the next chamber. A pre-cut plywood door assembly was used to reseal the nest chamber between visits. Nests were checked an average of once a week; near fledging, nests were checked every other day. Data collection is more likely to cause nest desertion early in the nesting cycle (i.e. before incubation) than after the eggs have hatched. In very early spring (1979), two nests were deserted, but in each case new, successful nests were made within the original territory.

RESULTS

Prey and foraging behavior.—Cyprinid species comprise the majority of the kingfisher's diet (Fig. 1A); stonerollers (*C. anomalum*) were observed most frequently. If, as suspected, a substantial proportion of the unidentified cyprinids in Fig. 1A are *C. anomalum*, this species would be under-represented in the figure. In addition, the percentage of crayfish (*Cambarus* spp.) may not reflect the importance of this species; 19 of the 21 observations of kingfishers bringing crayfish to the nest occurred during periods of high water and high turbidity when fish were difficult to catch.

The size range of fish taken by kingfishers is shown in Fig. 1B. Also shown is the "expected" distribution of prey, calculated from the proportion of each size class represented in the electroshocking data from Indian Creek (data are pooled from all territories). A Chi-square test showed no difference between the observed and expected sizes taken ($\chi^2 = 5.08$; $0.3 > P > 0.2$; df $= 4$), indicating that kingfishers take prey of different sizes in propor-

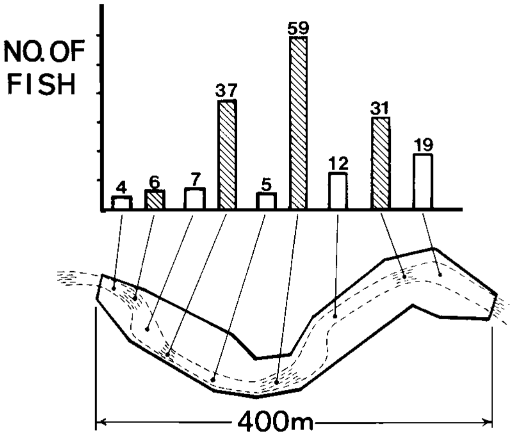

Fig. 2. Distribution of fish in pools and riffles of a typical nonbreeding territory. Hatched bars represent numbers of fish caught in riffle sections; open bars represent numbers of fish caught in pools.

tion to the relative abundance of each size. Appropriate data are not available to test adequately whether or not kingfishers select increasingly larger prey across the nesting season to feed their progressively larger young. The size distribution of the fish electroshocked in the nonbreeding season suggests that small fish are more abundant than would be predicted from the spring data ($\chi^2 = 79$, $P \geqslant 0.01$). It is unknown whether or not kingfishers take on-the-average smaller prey in the non-breeding season, but field observation confirms that they continue to feed mainly on fish (Davis 1980).

In both seasons, stonerollers are the most abundant prey species, comprising 70% of the total fish sampled by electroshocking in the nonbreeding season (data pooled from 1978 and 1979) and 72% in the breeding season; cyprinids other than stonerollers comprise 20% and 21%, respectively. There is no statistical difference in the proportion of stonerollers to "minnows" between seasons ($\chi^2 = 0.109$, $P > 0.7$, df = 1; total fish sampled in the nonbreeding season = 3,578, in the breeding season = 3,678), although noncyprinid species are more abundant in the non-breeding season ($\chi^2 = 32.68$, $P < 0.001$, df = 1). This relatively large proportion of stonerollers explains the large proportion of this species in the kingfisher's diet (Fig. 1A). Eipper (1956) also reports that stonerollers are a favorite prey of kingfishers.

During the initial electroshocking runs, the data from riffles and pools were combined. Although it was evident in the field that significantly more fish were taken from riffles, the initial data could not be analyzed to determine the difference in the number of fish occurring between these areas. Such data were available, however, for the 1,200 m of Indian Creek electroshocked in October 1979. Using these data, the distribution of prey species (fish) was found to be significantly greater in riffles than in pools ($n_{pool} = 12$, $\bar{x}_p = 48.65$ g/m; $n_{riffles} = 12$, $\bar{x}_r = 195.46$ g/m; $t = -3.11$, $P < 0.01$, df = 22; see example in Fig. 2). Stonerollers were most commonly found in the riffles ($\chi^2 = 234$, $P \leqslant 0.001$, df = 1), while other cyprinids, taken as a group, showed no preference for riffles or pools ($\chi^2 = 1.29$, $P > 0.2$, df = 1). *Campostoma anomalum* is known to be a riffle species (McClane 1978).

In the nonbreeding season, kingfishers use stream habitats differentially: during 80 observations, kingfishers were found fishing long riffles 71.3% of the time, along shallow pools 20% of the time, and at deep pools 8.7% of the time, despite the fact that riffles comprised only 36% of the stream's length ($\chi^2 = 35$, $P < 0.001$, df = 2). Unfortunately, foraging data were not collected for the breeding season, but my observations indicate that kingfishers behave similarly in the spring. Moreover, the predominant use of *C. anomalum* as food in the breeding season suggests that they fish primarily along riffles.

Territories.—Territories defended in the 1979 breeding season were more than twice as large as those defended in the 1979 nonbreeding season (breeding, $n = 6$, $\bar{x} = 1{,}030 \pm 219$ m; nonbreeding, $n = 21$, $\bar{x} = 389.29 \pm 92.63$; $t = 3.55$, $P \leqslant 0.005$, df = 31). The data are inconclusive as to whether or not food is a causal factor affecting territory size. For example, the size of nonbreeding territories is significantly inversely related to food density (g/m; $r^2 = -0.98$, $n = 6$, $P < 0.01$), while the size of breeding territories is not significantly correlated ($r = -0.71$, $n = 6$, $P > 0.05$). Care must be exercised when interpreting causal relationships from simple correlations: in both seasons, the negative correlations may result from the indirect effect of intruder pressure, i.e. more birds are attracted to higher food densities (Myers et al. 1980).

As mentioned previously, riffles contain significantly more fish than do pools, and kingfishers forage more often at riffles. If riffles are

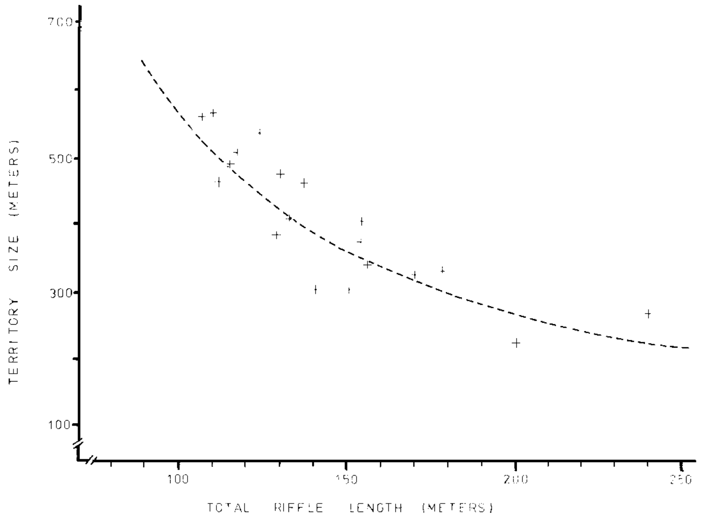

Fig. 3. Riffle length versus size of nonbreeding territories on Indian Creek, 1978. Riffle length and territory size are measured in meters. Data points fit an exponential equation (represented by the dashed line) with $r^2 = 0.75$, $n = 19$ and $P < 0.01$.

an important cue, one would expect territory size to be inversely related to total riffle length, as is the case (shown in Fig. 3) for nonbreeding territories ($n = 19$, $r^2 = 0.75$, $P < 0.01$). Although riffle length and breeding territory size are not significantly correlated ($n = 8$, $r = -0.45$, $P > 0.10$), breeding territories that have a greater concentration of riffles around the nest are significantly smaller than other territories, as is shown in Fig. 4 ($\bar{x} = 827.5$, $n = 4$; $\bar{x} = 1{,}213.75$, $n = 4$; $t = -3.76$, $P < 0.01$, df = 6). These results might be explained by postulating different functions for breeding and nonbreeding territories: nonbreeding territories appear to be essentially feeding territories, while breeding territories contain two important resources, food and a suitable nest site.

Nest-site limitation and reproductive success.—Suitable nesting banks appear to be in short supply. Of 24 banks along a 10.6-km section of Indian Creek, 13 banks were occupied by nesting pairs, 6 banks were unsuitable for occupation due to substrate characteristics (composed of a high percentage of clay and/or stone) or location near areas receiving much use by humans (e.g. dredging operations), and 5 banks remained unoccupied due to competitive exclusion by territorial individuals. Belted Kingfishers are not colonial nesters and will defend unoccupied nesting banks from conspecifics if they are within their territories. Starting in March, confrontations between males along sections of streams containing nesting banks were a common sight, suggesting the presence of more males than nesting banks. In addition, females seemed in surplus as well, because, on two occasions when the female of a pair disappeared, a new female took her place with the resident male. White (1953) and Hamas (1974) also reported nest-site limitations for the Belted Kingfisher. An estimate of the number of kingfishers competing for nests is not available due to the fact that birds were not banded until after territories were established.

Relationships of territory size and food abundance with reproductive success are summarized in Table 1. Significant correlations occur between the following sets of parameters: (1) territory size vs. average weight of fledglings ($r = 0.93$), and (2) food density (g/m) vs. number of birds fledged/nest ($r = 0.96$). The fact that food density (g/m) is significantly correlated with number of fledged/nest while territory size is not ($r = -0.45$) suggests that the size of the territory is less important than food density for production of offspring.

Discussion

Nest sites, food, and territory size.—Both the scarcity and location of nest sites in relation to riffles appear to influence territory establish-

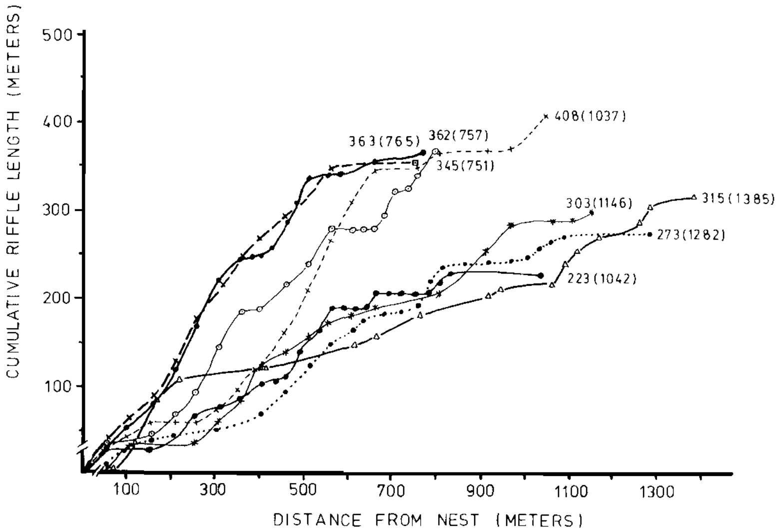

Fig. 4. Cumulative riffle length versus distance from nest. On the ordinate is the cumulative length of shallow water (depth ≤ 15 cm) as the distance from the nest increases symmetrically by 25 m on the abscissa. Data were obtained from detailed maps made of each territory, which included location and length of riffles and pools along the stream. Adjacent numbers represent total length of shallow water (primarily riffles), and numbers in parentheses represent lengths of territories.

ment by *Megaceryle alcyon*. Theoretically, nest-site limitations can suppress the breeding population density and thus lead to a lower level of competition for food than would occur if all potential breeders were able to nest. A scarcity of nest sites is often observed for birds (see Temple 1977), and field observations indicate competition for available nesting sites for kingfishers (Davis 1980). Accordingly, territoriality in the breeding season may primarily serve to secure a nest site, while the need to defend a food resource is secondary. This study presents data that support this hypothesis because territory size and food abundance (g/m) are not significantly correlated.

Other data, however, suggest that food distribution does influence the size of breeding territories, in that territory size appears to be established in a consistent relation to the proximity of productive food patches near the nest (Fig. 4), i.e. the smallest territories enclose the richest food sources. Hole-nesters typically select a nest site before establishing their territories (von Haartman 1957)—a generalization that accurately describes the Belted Kingfisher (Bent 1940, Davis 1980). Unless kingfishers evaluate food abundance during nest-site selection, my data imply that an element of chance enters into the equation that determines whether or not a particular pair of kingfishers will defend a large or small territory. Evidence is not in favor of a random selection of nest sites, however. First, males arrive at least a month before the females to find a suitable nesting bank (some males in mild winters remain the year around). Second, within most breeding territories along Indian Creek, more than one suitable nesting bank was available from which to choose.

In the event that food is concentrated near a nest site, defense of a small territory may save a pair time and energy both in defense of the territory and in the transport of fish back to the nest. To feed a nest full of young kingfishers may require considerable time and energy. Using data from Vessel (1978), I calculate that at maximum growth rate each nestling can consume approximately 11.2 fish/day. Given 15 h of daylight, each adult of a pair would need to catch 2.6 fish/h in order to feed seven young, not including fish for themselves. During unfavorable weather, this may be a difficult task, one that is aggravated if food is located far from the nests. As a result, access to an uncontested and rich food source may be critical for raising a full clutch of young kingfishers. As Seastedt and Maclean (1979) have pointed out for Lapland Longspurs, habitat quality may be better

TABLE 1. A summary of correlations (r) and significance levels between reproductive parameters, territory size, and food abundance. Sample size (n) varies due to the facts that not all territories were sampled for food or nest data were incomplete for some territories.

	Territory size			Food abundance					
				Grams/meter			Total grams		
	r	n	P	r	n	P	r	n	P
Number fledged/nest	−0.45	8	NS[a]	0.96	5	0.02	−0.27	5	NS
Average weight of fledglings per nest	0.93	7	<0.01	−0.50	5	NS	0.62	7	NS
Total weight of fledglings per nest	−0.22	7	NS	0.76	5	NS	−0.39	5	NS

[a] NS = $P > 0.05$.

represented by food density than by total quantity.

When food is not concentrated near the nest, it might be advantageous to defend as large a territory as possible, first, because larger territories may contain greater amounts of food (total biomass/territory) and, second, because larger territories may contain a more reliable food supply, i.e. a larger supply of alternative food resources. During fluctuations in water levels following heavy or prolonged rains, fishing becomes difficult, and kingfishers are obligated to switch to crayfish as prey, a food item not found in riffles. Perhaps as a consequence of both these factors, parents with larger territories that fledge the same number of offspring as those with smaller territories may produce heavier young. These increased fat reserves could increase the chances of survival of fledglings (Lack 1966), because the first few weeks after leaving the nest is a most critical period for young kingfishers. Early attempts at fishing are most often failures for the young birds, because they are weak flyers and apparently must learn how to fish (Bent 1940, White 1953, Davis 1980); the fact that parents continue to feed fledglings suggests that young have difficulty in obtaining their own food. Because *Megaceryle alcyon* typically raises only one clutch per year, the survival of fledglings may markedly affect the relative fitness of breeding pairs. It appears that assessing the relative value of large versus small territories in terms of reproductive success may depend upon environmental circumstances. As argued above, the weight at fledging may be important when the environment fluctuates, but fledging more but lighter young may increase fitness in a more constant, productive environment. Both strategies may be utilized by kingfishers, but the question of why kingfishers defend the sizes of territory that they do is still not answered.

There are two prevailing hypotheses that address the causal relationship between food abundance and territory size (Myers et al. 1980). The first is the "sufficient resource" hypothesis (see Verner 1977), which is derived from the classical concept that the basic function of territoriality is to secure adequate resources. This hypothesis states that individuals should defend only those resources that are required. The second hypothesis predicts that competition is most severe in areas of high resource density, leading to increased costs of defense; as a result, territory size is limited by competition for resources (Seastedt and Maclean 1979; Myers et al. 1979, 1980). Relevant data on the Belted Kingfisher are not yet available to enable a choice between these hypotheses; circumstantial evidence, however, favors the latter. Expansion of breeding territories was observed twice, once in 1978 (Davis 1980) and once in 1979, after an adjacent pair of kingfishers deserted their territory due to human interference at their nests. These observations support the hypothesis that breeding territory size is limited by competition. In a reverse sense, severe nest-site limitations may promote large breeding territories by reducing competition.

In the nonbreeding season, territories of individuals were remarkably constant in size. During prolonged rains, nonbreeding territories were often deserted but were reestablished by the original owners with the original boundaries when the water levels returned to normal. In December, some territories gradually increased in size as kingfishers began to disappear, presumably due to their migration south. When and how many birds migrated appeared to be related to the severity of the weather. During cold periods, accumulation of ice along the stream blocked access to fishing areas; the few birds remaining during the winter months (December–February) seemed to use crayfish more extensively, as gauged by the accumulation of their exoskeletons in the winter roosting nests examined. How dependent kingfishers are on crayfish in the winter is still unknown. Accumulation of exoskeletons may only indicate that these parts are not digestible while most parts of fish are digestible (White 1953). In terms of the proportion of digestible biomass/prey item, fish are probably a higher quality food item.

Proximate cues to assess resource abundance.—Although fish availability may fluctuate during the season (Davis 1980), particular habitat parameters associated with food may remain relatively constant, e.g. the amount of riffles present along a section of stream. Thus, if direct assessment of food by kingfishers is difficult, *Megaceryle alcyon* may instead respond to habitat parameters such as riffles. Morse (1976) believes that warbler species respond to cues that are easily monitored and are correlated to important factors. Similarly, data on Sparrowhawks (*Accipiter nisus*) (Newton et al. 1977) and Lapland Longspurs (Seastedt and Maclean 1979) indicate that these species respond to alternative habitat parameters rather than assessing food density directly. Other species are known to search for specific prey types by searching for specific sites or patches, rather than the prey item itself (Royama 1970, *Parus major*; Alcock 1973, *Agelaius phoeniceus*; Tinbergen 1976, *Sturnus vulgaris*). The Little Green Kingfisher (*Chloroceryle americana*) also prefers to fish along riffles within a stream habitat. Out of 62 observations made by the author in Costa Rica during the summer of 1981, the Green Kingfisher was found foraging along riffles 84% of the time. Kingfishers may not innately recognize riffles but instead learn to associate them with food by positive reinforcement subsequent to fishing success along riffles. Future experiments that manipulate food abundance are needed to determine the role of habitat parameters (riffles) in the assessment of habitat quality.

The general pattern displayed in Fig. 4 suggests that in addition to choosing a suitable nest site, breeding birds are able to use habitat cues as important parameters in establishing territory size. Only one pair defended a territory larger than expected, when size was predicted by the criterion of the cumulative length of riffles. This pair initially defended a smaller territory (approximately 830 m) but increased its size after the adjacent downstream territory was deserted due to human interference at the nest. In addition, the relationship between the size of nonbreeding territories and riffle length (Fig. 3) suggests that kingfishers may assess habitat quality (amount of food available) by observing the length of riffles present.

A "new" function of territoriality.—The view adopted in this study and held by most biologists is that territoriality evolved because defense of essential resources directly enhances the reproductive success of the defender (Nice 1941, Lack 1943, Hinde 1956, Brown 1964). But recently, it has been proposed that territorial behavior could also be adaptive by decreasing the success of one's reproductive competitors (Verner 1977). For example, if the cost of defense of a resource is minimal, the benefit in terms of relative reproductive success may be substantial if an individual can prevent conspecifics from obtaining a nest or food. A crucial assumption of the hypothesis of "superterritories" is that the cost of defense is not prohibitive. Along this line, Rothstein (1979) argues for the evolution of "inhibitory traits," like aggression, in animals that use specialized nest sites or utilize highly concentrated food resources. In the present study, 28% of the available nest sites appeared to remain unoccupied due to exclusion of potential nesters by extant territory owners. Such aggressive behavior, characteristic of territoriality in *Megaceryle alcyon*, could be an "inhibitory trait" as described by Rothstein. If so, territoriality in this species may be adaptive not only because it secures resources essential to survival, but also because it excludes competitors from resources that are not utilized by a defender.

Several investigators (Getty 1979, Pleasants and Pleasants 1979) have voiced strong criticism of this hypothesis. More empirical studies are needed to determine whether or not animals do defend territories larger than are needed to fulfill their own requirements. More extensive data on reproductive success and territory size are required, and animals that have specialized nest-site or food requirements that are easily defended should be critically evaluated.

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SHORT COMMUNICATIONS

Eggshell Strength and Cowbird Parasitism of Red-winged Blackbirds

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Recently, there has been much interest in avian brood parasitism (review by Payne 1977). Its study provides a unique opportunity to gain some understanding of how two distinct and different lineages coevolve (Robertson and Norman 1977). Rothstein (1975) suggests that, during the egg-laying period, host species for the Brown-headed Cowbird (*Molothrus ater*) fall into two mostly nonoverlapping categories: some species, "rejecters," exhibit behaviors that, at least in part, negate the efforts of the parasite, while others, "accepters," appear to tolerate the presence of cowbird eggs.

In 1975 and 1976 we monitored cowbird parasitism in populations of an accepter species, the Red-winged Blackbird (*Agelaius phoeniceus*), in Lincoln County, South Dakota. Rates of parasitism measured at the beginning of incubation were 14 out of 19 nests (21 out of 90 eggs) in 1975 and 14 out of 34 nests (23 out of 136 eggs) in 1976. These results confirm other published reports that Red-winged Blackbirds are common cowbird hosts on the Great Plains (Hergenrader 1962, Hill 1976, Facemire 1980). The higher rate of parasitism in 1975 might have resulted from a drought-induced reduction in the number of available host nests.

Apparently, Brown-headed Cowbird nestlings show few adaptations for the parasitic habit. They do not hatch significantly sooner than host nestlings, their growth rates are similar to those of related species (Payne 1977), and they do not evict nest mates. Recently, Eastzer et al. (1980) have shown that cowbird nestling survival in Barn Swallow (*Hirundo rustica*) nests was no better than four of five nonparasitic species, although a fledgling cowbird was successful in eliciting feeding behavior from Barn Swallow foster parents.

Cowbird nestlings often do enjoy a competitive advantage, however, because they typically occur in the nests of smaller host species. Another strategy for gaining a disproportionately large share of food resources involves a reduction in the number of competing host nestlings. One way cowbirds accomplish this is by removing host eggs. We examined our 1975 and 1976 samples of Red-winged Blackbird nests for evidence of host-egg removal (Table 1). If one assumes a normal clutch size of four, then cowbirds at 10 of the 37 parasitized nests showed no ejection behavior. Because in the remaining nests a number of Red-winged Blackbird eggs may have disappeared for other reasons (see below), we conclude that cowbirds quite often fail to eject Red-winged Blackbird eggs.

We suggest that cowbirds have evolved an additional kind of indirect strategy to reduce the number of competing Red-winged Blackbird nestlings. This strategy involves eggshell strength and egg survivorship. We suggest that Red-winged Blackbird eggs are structurally weaker and more likely to be broken (and subsequently removed) during egg-laying and incubation than are cowbird eggs. As part of a 1979 and 1980 study of egg porosity in these two species, we used the scanning electron microscope to measure shell thickness in eggs collected before the onset of incubation. The thickness measurement for each egg was the mean of five shell fragments near the equator of the egg. Thickness measurements did not include the shell membranes. Thirty Red-winged Blackbird eggs (mean fresh weight = 4.03 g ± 0.43 SD) had a mean thickness of 41.38 μm ± 3.56 SD, while 30 cowbird eggs (mean fresh weight = 3.26 g ± 0.24) had a mean thickness of 58.79 μm ± 2.67. Thus, using thickness as one measure of shell strength, we conclude that cowbird eggs are clearly stronger. The fact that the heavier Red-winged Blackbird eggs had thinner eggshells runs counter to the usual relationship between egg weight and shell thickness in birds (Ar et al. 1974).

But, in fact, are Red-winged Blackbird eggs more likely to be cracked and broken? During the porosity study, a number of eggs of both species had unexpectedly high rates of water loss. Upon close examination, these eggs were determined to have cracks. Because all eggs were wrapped in cotton wadding before being transported from the field to the laboratory, we are confident that most of these eggs were already cracked in the nest. The numbers of cracked eggs in parasitized nests were as follows: 1979, 23 of 65 (35.4%) Red-winged Blackbird eggs and 14 of 81 (17.3%) cowbird eggs; 1980, 35 of 89 (39.3%) Red-winged Blackbird eggs and 19 of 151 (12.6%) cowbird eggs. Pooling the data for both years, the proportion of cracked eggs in Red-winged Blackbirds was significantly higher ($\chi^2 = 36.41$, df = 1, $P < 0.005$).

Presumably, an individual egg is cracked either by being stepped on by the female or by being jostled against other eggs. In both cases, eggs with thicker, stronger shells (i.e. cowbird eggs) would enjoy a distinct advantage. With regard to egg jostling, it is expected that, when a Red-winged Blackbird egg is jostled against a thicker-shelled cowbird egg, it is more likely to crack than when it is jostled against another Red-winged Blackbird egg. This idea can be tested by comparing the numbers of cracked Red-winged Blackbird eggs in parasitized and nonpar-

TABLE 1. Nest contents at the beginning of incubation or at the time of nest discovery.

	Number of nests	
Nest contents[a]	1975	1976
5 RW	—	1
4 RW	4	17
4 RW, 1 CB	5	3
4 RW, 2 CB	—	1
4 RW, 3 CB	1	—
3 RW	3	7
3 RW, 1 CB	4	4
3 RW, 2 CB	4	5
3 RW, 3 CB	—	1
2 RW	—	2
2 RW, 1 CB	1	2
2 RW, 2 CB	1	2
2 RW, 4 CB	1	—
1 RW, 1 CB	—	1
1 RW, 4 CB	1	—

[a] RW = Red-winged Blackbird eggs; CB = Brown-headed Cowbird eggs.

asitized nests. Ideally, only eggs from clutches of equal size should be used for such comparisons. Because no sample for a single clutch-size category was sufficiently large, we included eggs from all clutch-size categories in our analysis. The numbers of cracked eggs were as follows: 1979, 35 of 89 (39.3%) in parasitized nests and 33 of 120 (27.5%) in nonparasitized nests; 1980, 58 of 154 (37.6%) in parasitized nests and 50 of 230 (21.7%) in nonparasitized nests. Pooling the data for both years, the number of cracked eggs was significantly higher in parasitized nests ($\chi^2 = 11.57$, df = 1, $P < 0.005$).

We have demonstrated that by the time incubation begins a significantly larger number of Red-winged Blackbird eggs sustains cracks than do cowbird eggs. It remains to be demonstrated that Red-winged Blackbird eggs actually survive less well in the field during incubation. Our assumption is that most cracked eggs subsequently break and are removed from the nest. In 1975 and 1976 during incubation, we visited parasitized and nonparasitized nests almost every day and were able to compare egg survivorship in the two species. Eggs that were lost because of whole-nest predation were not included in the comparison. Typically, single eggs would disappear from a nest between one visit and the next. In 1975, 14 Red-winged Blackbird eggs were lost during 580 egg-days, while no cowbird eggs were lost during 245 egg-days. In 1976, disregarding two cowbird eggs that were laid maladaptively during incubation, 13 Red-winged Blackbird eggs were lost during 691 egg-days while 1 cowbird egg was lost during 181 egg-days. The difference between rates of egg loss for the two species was tested by using a test of proportions (Ferguson 1966: 176). Pooling data across 1975 and 1976 and using a one-tailed test, egg loss was significantly greater in Red-winged Blackbirds ($Z = 2.65$; $P < 0.01$). Eighteen of the 27 eggs lost (66.7%) were in parasitized nests.

We believe this differential egg loss was due to a greater tendency for Red-winged Blackbird eggs to break and to be subsequently ejected by female Red-winged Blackbirds. There are alternative explanations, however, that need to be examined. Because cowbird eggs are better camouflaged, it could be argued that differential egg survivorship was due to a greater probability of Red-winged Blackbird eggs being preyed upon during partial predation. Picman (1977) demonstrated that the Long-billed Marsh Wren (*Cistothorus palustris*), a common breeding species in the study area, does break and remove Red-winged Blackbird eggs. His results, however, indicate that Marsh Wrens respond equally to eggs of a different color. It may also be argued that female cowbirds remove some Red-winged Blackbird eggs after incubation has begun. Although such behavior has been observed by Mayfield (1961) in the Kirtland's Warbler (*Dendroica kirtlandii*), it apparently occurs only rarely, because cowbirds usually lay an egg of their own after removing a host egg and such eggs laid after incubation essentially would be wasted.

From the parasite's point of view, it is surprising that the Red-winged Blackbird is used so often as a host, because cowbird nestlings would be expected to do better in the nests of smaller hosts. The negative effect of large host size, however, can be countered by reducing the number of host eggs (and therefore host nestlings). Cowbirds often do this by ejecting host eggs. An additional, favorable change in the ratio of host to parasite eggs would occur if host eggs had lower survival rates during incubation. This study indicates that such is the case when Red-winged Blackbirds serve as hosts, primarily because Red-winged Blackbird eggs are structurally weaker.

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Evidence of a Boreal Avifauna in Middle Tennessee during the Late Pleistocene

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A faunistically significant, stratified cave deposit was discovered during an archaeological site survey of the proposed Tennessee Valley Authority (TVA) Columbia Dam reservoir that will impound approximately 30 km of the Duck River in middle Tennessee. This small cave, known as Cheek Bend Cave (40MU261), is in a limestone bluff 20 m above the river bed, 13 km east-southeast of Columbia, Maury County. Testing for the presence of aboriginal occupation began in September 1978 and, as a result of encountering huge quantities of animal bone and shell at considerable depths that appeared not to be attributable to man, was continued until May 1979. Three 1 × 2-m excavation units placed along the east wall revealed stratified deposits of animal remains to a depth of about 4.5 m.

On the bases of the species composition within and among strata, differing fill zones, and certain other stratigraphic features, the deposit reflects two distinct and well-defined major episodes of fill. The top 2 m represent the Holocene epoch and contain remains of only extant modern species. In contrast, the faunal assemblage in the bottom 2 m, although it includes some species that still inhabit the cave area (presently a deciduous Western Mesophytic Forest), contains many that are now extirpated and reflect a prairie habitat (Prairie Chicken, *Tympanuchus cupido*; 13-lined ground squirrel, *Spermophilus tridecemlineatus*, pocket gopher, *Geomys* sp.) or a boreal environment (e.g. arctic shrew, *Sorex arcticus*; water shrew, *Sorex palustris*; red-backed vole, *Clethrionomys gapperi*; yellow-cheeked vole, *Microtus xanthognathus*; red squirrel, *Tamiasciurus hudsonicus*; northern flying squirrel, *Glaucomys sabrinus*; and heather vole, *Phenacomys intermedius*). Recovery of a partial carapace of a wood turtle (*Clemmys insculpta*) also suggests, based on the present center of distribution of the wood turtle, a well-established boreal environment for an extended period of time in this area during the Late Wisconsinan (Parmalee and Klippel 1981).

The avifauna from Cheek Bend Cave is extremely diversified and reflects both open grassland or savanna and forest habitat. Remains of aquatic birds (e.g. Pied-billed Grebe, *Podilymbus podiceps*, and at least three species of ducks) are rare in the deposit, although several species associated with riverine or marsh habitats are represented. Most notable among these are the Yellow Rail (*Coturnicops noveboracensis*) and the Black Rail (*Laterallus jamaicensis*), both probably rare transients in Tennessee, although their modern distribution in the Midsouth is poorly known. We identified a minimum of approximately 60 species, representing 28 families, from the avian sample. Elements of numerous passerine species of the families Parulidae and, particularly, Fringillidae comprised 75–95% of the avian samples from the Holocene levels. Except for the Passenger Pigeon (*Ectopistes migratorius*) and the Ruffed Grouse (*Bonasa umbellus*), all of the identified species represented in the Holocene levels are still a part of the avifauna of middle Tennessee. A comprehensive report dealing with the stratigraphy and chronology of Cheek Bend Cave, its archaeological component, and the total faunal assemblage is being prepared for the Tennessee Valley Authority.

Several species of birds identified from elements recovered in the bottom 2 m of the deposit are especially significant, because they not only represent new state or regional records but also because they suggest a boreal climate and habitat in this region during the Wisconsinan. Five species worthy of special comment are the Hawk Owl (*Surnia ulula*), Boreal Owl (*Aegolius funereus*), Saw-whet owl (*Aegolius acadicus*), Gray Jay (*Perisoreus canadensis*), and Pine Grosbeak (*Pinicola enucleator*). In addition to these

TABLE 1. Avian species identified from the late Pleistocene strata of Cheek Bend Cave, Maury County, Tennessee.

Falconidae
- American Kestrel, *Falco sparverius*

Tetraonidae
- Ruffed Grouse, *Bonasa umbellus*
- Sharp-tailed Grouse, *Pedioecetes phasianellus*[a]
- Greater Prairie Chicken, *Tympanuchus cupido*

Rallidae
- Yellow Rail, *Coturnicops noveboracensis*

Scolopacidae
- Common Snipe, *Capella gallinago*[a]
- American Woodcock, *Philohela minor*

Columbidae
- Passenger Pigeon, *Ectopistes migratorius*

Strigidae
- Barred Owl, *Strix varia*
- Boreal Owl, *Aegolius funereus*[a]
- Saw-whet Owl, *Aegolius acadicus*[a]
- Hawk Owl, *Surnia ulula*[a]

Apodidae
- Chimney Swift, *Chaetura pelagica*[a]

Picidae
- Common Flicker, *Colaptes auratus*[a]
- Red-bellied Woodpecker, *Melanerpes carolinus*
- Hairy Woodpecker, *Picoides villosus*

Tyrannidae
- Eastern Phoebe, *Sayornis phoebe*

Alaudidae
- Horned Lark, *Eremophila alpestris*[a]

Corvidae
- Blue Jay, *Cyanocitta cristata*
- Gray Jay, *Perisoreus canadensis*[a]

Sittidae
- Red-breasted Nuthatch, *Sitta canadensis*[a]

Turdidae
- Robin, *Turdus migratorius*

Icteridae
- Meadowlark, *Sturnella* sp.

Fringillidae
- Purple Finch, *Carpodacus purpureus*
- Pine Grosbeak, *Pinicola enucleator*[a]
- Pine Siskin, *Carduelis pinus*[a]
- cf. Towhee, *Pipilo erythrophthalmus*
- cf. White-throated Sparrow, *Zonotrichia albicollis*

[a] Remains present only in late Pleistocene strata.

five, remains of 23 other species were identified from the late Pleistocene strata (Table 1). In addition to the three owls, Gray Jay, and Pine Grosbeak, the Red-breasted Nuthatch (*Sitta canadensis*) and Pine Siskin (*Carduelis pinus*) also suggest extensive coniferous forests in the vicinity of Cheek Bend Cave. Although most species comprising the avian assemblage reflect a forest habitat, the presence of meadowlark (*Sturnella* sp.), Horned Lark (*Eremophila alpestris*), Prairie Chicken, Sharp-tailed Grouse (*Pedioecetes phasianellus*), and some rodents such as the pocket gopher (*Geomys* sp.) is indicative of these forested areas having been interspersed with shortgrass prairie or savanna.

The Hawk Owl lives in Canada and Alaska in coniferous forests mixed with birch scrub, tamarack bogs, and muskegs (Bent 1938). This owl is a rare and sporadic winter vagrant in northern Plains and Midwest states; there are no historic records of it from Tennessee and no Pleistocene records from anywhere. Identification of *Surnia ulula* from Cheek Bend Cave is based on a complete phalanx (phalanx I, digit I) and premaxilla (Fig. 1). Distribution of the Boreal Owl is similar to that of the Hawk Owl, as is its choice of habitat. The only fossil (Holocene?) record of *A. funereus* is from Shelter Cave, New Mexico (Brodkorb 1971). Evidence of its occurrence in historic times in Tennessee is lacking. Diagnostic elements of at least two individuals of the Boreal Owl from Cheek Bend Cave consist of the proximal two-thirds of a right and shaft section of a left tarsometatarsus, distal one-third of a right and distal end of a left tibiotarsus, distal end of a right femur, head of a left humerus, distal end of a left ulna, proximal end of a left radius, sections of a lower jaw, articular end of a left scapula, coricoidal articular facet and manubrium section of a sternum, and 18 phalanges.

Although the Saw-whet Owl is not restricted to the northern coniferous forests, its center of distribution and greatest abundance lies in the woodland areas across southern Canada, the Great Lakes states, and in the northeastern United States. It is a rare winter resident in the Midsouth; there are only four reported sight records of this owl in the Nashville area (ca. 60–80 km north of Cheek Bend Cave) (Riggins 1977). All remains of *A. acadicus* were recovered from the same late Wisconsinan levels (300–400 cm below the surface) in which the bones of the Hawk Owl and Boreal Owl occurred. Remains of the Screech Owl (*Otus asio*), a common inhabitant of primarily deciduous forests of eastern North America, were found in the Holocene levels of Cheek Bend Cave but not in the Pleistocene levels. Elements of the Saw-whet Owl consist of the distal section of a right and left coracoid, articular end of a right scapula, proximal one-half of a right and distal one-third of a left radius, distal end of a left ulna, a complete right tibiotarsus, distal one-third of a right tarsometatarsus, and seven phalanges.

In eastern North America both the Gray Jay and Pine Grosbeak occur throughout the coniferous forests of southern Canada, and in the United States they seldom appear farther south than the upper Great Lakes and northern New England states. Like

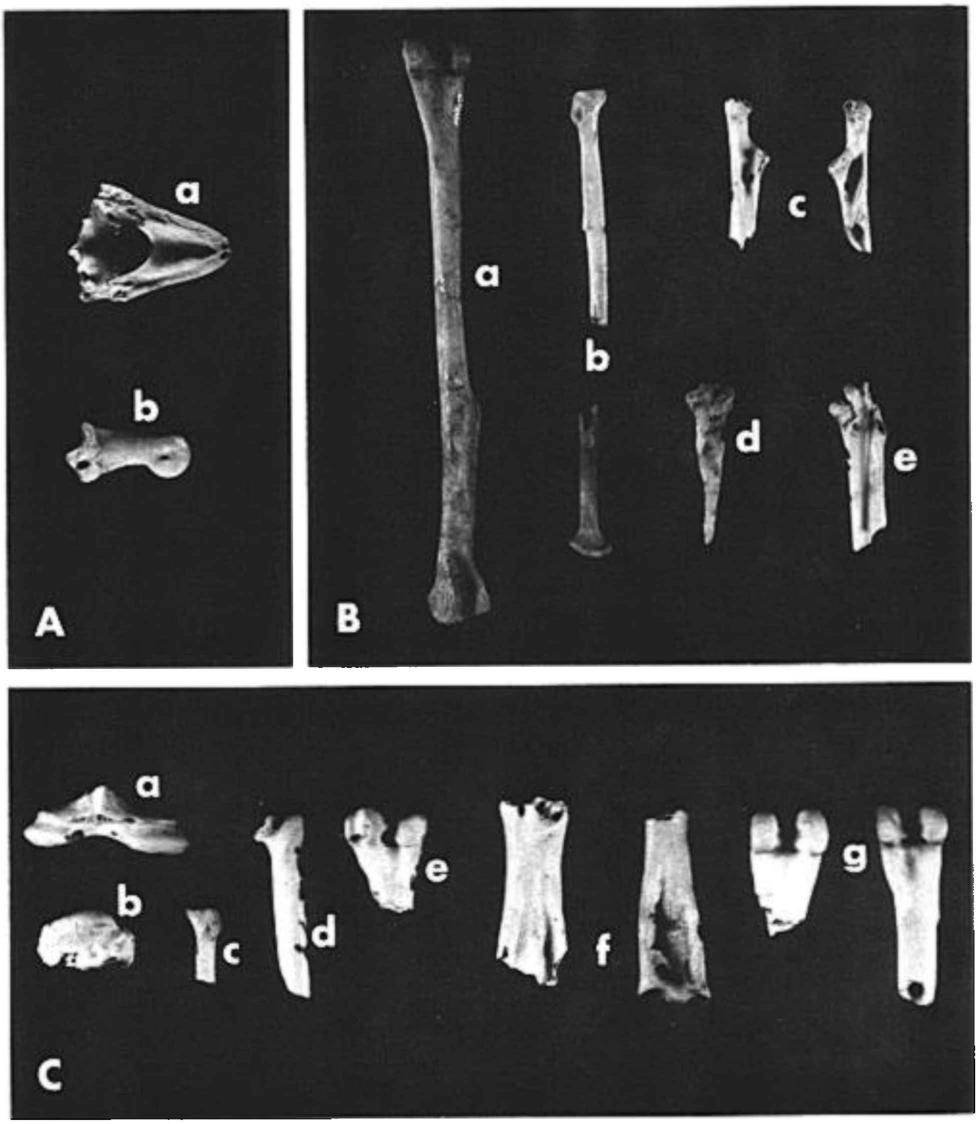

Fig. 1. Avian fossils from Cheek Bend Cave, Maury County, Tennessee. A. *Surnia ulula*: a, premaxilla; b, phalange. B. *Aegolius acadicus*: a, tibiotarsus; b, radii; c, coracoids; d, ulna; e, tarsometatarsus. C. *Aegolius funereus*: a, sternum; b, humerus; c, radius; d, ulna; e, femur; f, tarsometatarsi; g, tibiotarsi.

the Hawk Owl and Boreal Owl, these two passerines are associated with a boreal habitat and seldom wander or migrate great distances. Identification of *Pinicola enucleator* was based on sections of the lower jaw and left carpometacarpus (distinct from *Pheuticus* and *Hesperiphona*) and that of *Perisoreus canadensis* on limb elements including the distal ends of two left humeri and two complete left carpometacarpi. Fossil records of these passerines are lacking (Brodkorb 1978).

In a recent study of the late Pleistocene vegetation of the eastern Highland Rim and Cumberland Plateau, based on the analyses of pollen recovered from sediment cores from Anderson Pond (White County) and Mingo Pond (Franklin County), Delcourt (1979) was able to show that several major vegetational changes have taken place during the past 25,000 years. During the Wisconsinan glacial maximum, about 19,000–16,300 yr BP, boreal taxa of jack pine, spruce, and fir were dominant, and "Between 16500 and 12500 yr BP, mixed coniferous deciduous forests covered the landscape between 34°N and 37°N latitude" (Delcourt 1979: 276). In his discussion of the vegetation of eastern North America 18,000 yr ago, Wright (1981: 122) states that "Boreal forest formed a belt perhaps 1000 km broad, starting at or near the [Laurentide] ice front in the north and ending south near a line extending from central Georgia around the southern end of the Appalachian Highlands to Tennessee . . . ." Recovery of remains of predominately boreal small mammals from the lower levels of Cheek Bend Cave and those of four avian species whose present primary northern ranges coincide, coupled with pollen analyses data, suggest that the Nashville Basin was characterized by climatic conditions that included somewhat lower annual mean temperatures than exist today and a climax vegetation dominated by coniferous forest. Although the possibility exists that the former presence of the Hawk Owl, Boreal Owl, Saw-whet Owl, Gray Jay, and Pine Grosbeak at this cave site was the result of southward-wandering vagrants, the small mammal assemblage and the remains of at least two individuals of *A. funereus* and *P. canadensis* suggest a locally established population of these boreal birds during the Wisconsinan.

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Flightlessness in Flying Steamer-Ducks

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Steamer-ducks comprise a single, widely distributed, flying species, *Tachyeres patachonicus* (Falklands and Fuego-Patagonia), and three flightless species, *T. brachypterus* (Falklands), *T. pteneres* (Tierra del Fuego and the southern coast of Chile), and the recently discovered (Humphrey and Thompson 1981) *T. leucocephalus* (coast of Chubut, Argentina). This paper presents data on wing loading and use of flight for escape by Flying Steamer-Ducks and evidence that some individuals are permanently incapable of flight.

Flying Steamer-Ducks occur in freshwater and marine coastal environments in Patagonia, Tierra del Fuego, and the Falkland Islands (Weller 1976, Humphrey and Thompson 1981). They feed on sessile or slow-moving molluscs, crustaceans, and insect larvae, which they often obtain by diving, using hind feet and partly spread wings for propulsion (Murphy 1936: 960; Humphrey and Livezey unpubl. data).

Weller (1976: 47) noted the "hesitancy of . . . Flying Steamer Ducks to fly . . . ." Murphy (1936: 970), writing of Beck's collecting activities, stated that Flying Steamer-Ducks "are capable of getting well into the air within a space of 2 meters, even in a dead calm," and "they rarely dived at the approach of . . . [Beck's] craft, but preferred to take wing. . . . some of them flew heavily, not rising far above the water, while others mounted high into the air and passed quite out of sight." Reynolds (*in* Lowe 1934: 474) wrote that "*Tachyeres patachonicus* is capable of sustained and rapid if somewhat heavy flight. . . . At times *T. patachonicus* may well be taken for a flightless bird, and some of the confusion distinguishing between the two species [*patachonicus* and *pteneres*] is probably due to the unaccountable reluctance to rise so often demonstrated by this species."

During field seasons in 1979 (Humphrey and Max C. Thompson) and 1980–1981 (Humphrey and Livezey), 57 specimens of Flying Steamer-Ducks were collected near Ushuaia, Tierra del Fuego (5–17 November 1979, 24–27 December 1980, 4–6 January 1981), Puerto Deseado, Province of Santa Cruz (10–16 October 1979, 20–26 January 1981), and Puerto Melo,

TABLE 1. Weights, wing areas, and wing loadings of Flying Steamer-Ducks by sex and locality.

Locality and latitude	Sex	Weight (g)			Wing area (cm²)			Wing loading (g/cm²)		
		n	Mean	Range	*n*	Mean	Range	*n*	Mean	Range
Puerto Melo, 44°01′	Males	1	2,350	—	1	1,160	—	1	2.03	—
	Females	0	—	—	0	—	—	0	—	—
	Total	1	2,350	—	1	1,160	—	1	2.03	—
Puerto Deseado, 47°46′	Males	16	2,994	2,350–3,350	11	1,307	1,076–1,422	11	2.29	2.03–2.53
	Females	18	2,416	1,950–2,900	14	1,207	1,090–1,290	14	1.95	1.65–2.35
	Total	34	2,688	1,950–3,350	25	1,251	1,076–1,422	25	2.10	1.65–2.53
Ushuaia, 54°48′	Males	10	3,155	2,800–3,480	10	1,272	1,156–1,358	10	2.49	2.21–2.83
	Females	10	2,440	2,150–2,650	8	1,243	1,124–1,369	8	1.98	1.75–2.13
	Total	20	2,798	2,150–3,480	18	1,259	1,124–1,369	18	2.26	1.75–2.83
All localities	Males	27	3,029	2,350–3,480	22	1,284	1,076–1,422	22	2.37	2.03–2.83
	Females	28	2,425	1,950–2,900	22	1,220	1,090–1,369	22	1.96	1.65–2.35
	Total	55	2,722	1,950–3,480	44	1,252	1,076–1,422	44	2.17	1.65–2.83

Province of Chubut (29 September 1979), Argentina. We recorded details of escape behavior while each bird was being pursued during 1980–1981; limited data of the same kind were recorded during 1979. We collected 44 Flying Steamer-Ducks for which wing-loading data could be recorded; for 30 of these, we recorded whether or not they flew, and we have information on wind conditions at the time of collection for 21. Each specimen was weighed within 2 h following collection, and additional data were recorded, including: outline of fully extended wing (Raikow 1973: 297), weight of contents of esophagus and gizzard, sex, gonad measurements, weight of pectoral musculature, and molt. Wing area for each

TABLE 2. Mean weights, wing areas, and wing loadings of 22 species of diving-ducks. Sources: (1) Hartman 1961, (2) Magnan 1912, (3) Magnan 1913, (4) Magnan 1922, (5) Meunier 1951, (6) Müllenhoff 1885, (7) Poole 1938, (8) Raikow 1973.

Species	*n*	Weight (g)	Wing area (cm²)	Wing loading (g/cm²)	Source
Aythya affinis	20	615	474	1.30	1, 7, 8
A. collaris	3	757	460	1.65	7
A. ferina	1	842	615	1.37	6
A. fuligula	1	741	474	1.56	6
A. marila	1	675	621	1.09	6
A. nyroca	2	510	577	0.88	3, 6
A. valisineria	1	910	701	1.30	8
Bucephala albeola	6	393	341	1.16	7, 8
B. clangula	5	748	539	1.40	4, 6, 8
Clangula hyemalis	2	980	551	1.78	6, 7
Melanitta fusca	4	1,320	866	1.52	2, 5, 8
M. nigra	1	870	679	1.28	4
M. perspicillata	1	827	649	1.27	8
Lophodytes cucullatus	1	630	401	1.57	Present study
Mergus albellus	1	495	431	1.15	4
M. merganser	1	1,470	853	1.72	4
M. serrator	1	818	589	1.39	4
Oxyura dominica	7	363	352	1.03	1
O. jamaicensis	13	530	331	1.60	7, 8
Somateria fischeri	1	1,457	719	2.03	8
S. mollissima	2	2,056	1,210	1.79	5, 8
S. spectabilis	1	1,700	824	2.06	8

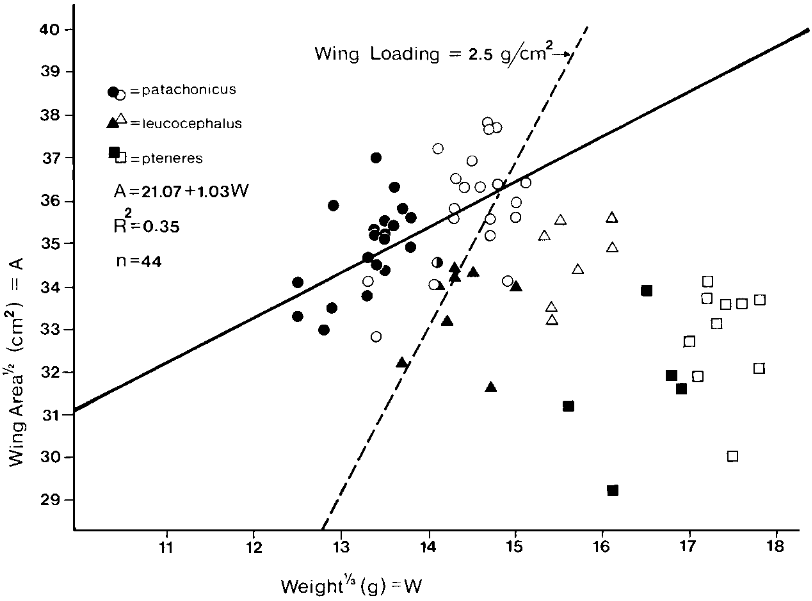

Fig. 1. Regression of cube root of body weight and square root of wing area for 44 Flying Steamer-Ducks. Open symbols represent males, black symbols females. Data for flightless *T. leucocephalus* (15) and *T. pteneres* (15) were not used in calculating the regression equation. Note that, except for four female *leucocephalus*, all points for the two species of flightless steamer-ducks fall to the right of the dashed line representing the threshold of flightlessness and have wing areas below those predicted by the regression equation calculated for *T. patachonicus*.

specimen was measured using a planimeter and doubled to give total wing area. Wing loading in g/cm² was calculated by dividing total weight by total wing area.

Wing loadings of 44 Flying Steamer-Ducks averaged 2.17 g/cm² (Table 1). Based on major reviews of wing loading (Müllenhoff 1885, Banks 1933, Poole 1938, Savile 1957, Hartman 1961, Greenewalt 1962, Raikow 1973), Flying Steamer-Ducks have among the highest wing loadings recorded for flying birds.

The relationship between means of wing area and body weight in 23 species of diving-ducks, including *T. patachonicus* (Tables 1 and 2), is expressed in the power equation:

$$\text{Wing Area} = 7.36\ \text{Weight}^{0.65}\ (R^2 = 0.85,\ n = 23)$$

and thus approximates the expected, wherein the allometric coefficient is 0.67, given that wing area increases as the square and body weight as the cube. The relationship between wing area and body weight for Flying Steamer-Ducks is negatively allometric:

$$\text{Wing Area} = 147.4\ \text{Weight}^{0.27}\ (R^2 = 0.36,\ n = 44).$$

Wing areas of two species of flightless steamer-ducks (*T. pteneres, T. leucocephalus*) are below those expected from the linear regression of the square root of wing area on the cube root of weight calculated for Flying Steamer-Ducks (Fig. 1). In addition, wing loadings of flightless steamer-ducks are for the most part much higher; wing-loading values of heavy male *T. patachonicus* overlapped those of female *T. leucocephalus* with low body weights (Fig. 1).

Weights and wing loadings of Flying Steamer-Ducks differed between sexes and among the three localities of collection (Table 1). Males averaged heavier than females at Puerto Deseado ($t = 6.19$, $P < 0.001$) and Ushuaia ($t = 7.94$, $P < 0.001$). Extreme weights of males and females overlapped at Puerto Deseado but not at Ushuaia (Table 1). Weller (1976: 47) found no overlap in weight between sexes of three species of steamer-ducks. Males also exceeded females in wing area at Puerto Deseado ($t = 2.88$, $P < 0.005$) but not at Ushuaia ($t = 0.87$, $P < 0.20$). Also, male Flying Steamer-Ducks were heavier ($t = 1.75$, $P < 0.05$) at higher-latitude Ushuaia than at Puerto Deseado, in agreement with Bergmann's Rule (James 1970, McNab 1971); females, however, were similar in weight at the two localities ($t = 0.24$, $P > 0.40$).

Of 22 male specimens (not in wing molt) collected in 1979 and 1980–1981, six had wing loadings of 2.5 g/cm² or greater, the limit beyond which Meunier (1951: 430) estimated aerial flight to be impossible. The highest wing loadings of birds known to have flown were 2.25 and 2.43 g/cm^2; both birds were males and were collected on windy days. We collected seven birds, all males, with wing loadings of 2.25 g/cm^2 and greater that swam, steamed, or dived but did not fly when pursued by a noisy motorboat. Two of the birds had slight amounts (34 g, 35 g) of food in esophagus and gizzard and the rest only clean grit (average 15 g, range 9–22 g). Of the latter, two had wing loadings above 2.6 g/cm^2; both had little fat, flightworthy remiges, and pectoral musculature at or near maximum weight (17% of body weight; pers. data). One was collected on a calm day and the other in a strong wind when other steamer-ducks were flying. We believe these birds were incapable of flight.

Assuming the validity of Meunier's (1951) flightlessness threshold of 2.5 g/cm^2, 50% of the nonmolting males we collected near Ushuaia were flightless, as were 8% of those collected near Puerto Deseado. The higher incidence of flightless males in the south is related to greater body weights and resultant higher wing loadings. Nevertheless, at both localities most male Flying Steamer-Ducks with wing loadings below 2.5 g/cm^2 are close to the threshold of flightlessness (Fig. 1).

We weighed the contents of gizzard and esophagus of all specimens collected in 1980–1981; maximum weight of gizzard and esophageal contents of Flying Steamer-Ducks was 176 g, and mean weight (n = 32) was 32 g. Because our measure of weight of ingested food did not include intestinal contents, the maximal weight of food ingested per feeding bout is probably twice (or more) the 176 g measured for contents of esophagus and gizzard, or 350+ g.

Sixteen male Flying Steamer-Ducks had wing loadings of less than 2.5 g/cm^2. We calculated the weight increase needed for each of these birds to have a wing loading of 2.5 g/cm^2. The mean increase required was 304 g, and for 11 birds the increase needed was less than 350 g. Therefore, we hypothesize that approximately 64% of male Flying Steamer-Ducks at Puerto Deseado and 80% at Ushuaia that are not already functionally flightless for other reasons (wing molt, wing loading of 2.5 g/cm^2 or greater) could become temporarily flightless because of weight gained from ingested food.

A strategy that would avoid substantial temporary increases in weight from feeding would be to eat small amounts of food at any one time and to feed often during the day. Weller (1976: 49) stated that "flightless forms [*pteneres, brachypterus*] take large food items in brief but intense feeding periods, whereas Flying Steamer Ducks seem to feed more continuously on smaller items."

We conclude that the threshold of flightlessness in Flying Steamer-Ducks is at wing loadings of approximately 2.5 g/cm^2. Roughly 25% of male *T. patachonicus* exceed this threshold and approximate the wing loadings of the lightest of their flightless congeners. Depending on the availability of wind, Flying Steamer-Ducks may be reluctant to fly with wing loadings as low as 2.3 g/cm^2; they are unable to fly with wing loadings of 2.5 g/cm^2 and above. Wing loadings and incidence of flightlessness in Flying Steamer-Ducks are higher in males and in birds from higher latitudes.

We are now investigating factors that affect weight, wing area, and wing loading of steamer-ducks and testing hypotheses concerning the morphology, adaptive significance, and evolutionary origins of flightlessness in *Tachyeres.*

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Observations on migratory Turkey Vultures and Lesser Yellow-headed Vultures in northern Colombia

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Turkey Vultures (*Cathartes aura*) breed from southern Canada to Tierra del Fuego, while Lesser Yellow-headed Vultures (*Cathartes burrovianus*) occur from México through Central America to northern Argentina and Uruguay (Meyer de Schauensee 1966). It has long been known that Turkey Vultures breeding in the northern parts of their range are migratory, and data are available on their arrival at or departure from their breeding grounds in spring or fall (Bent 1937). Likewise, parts of their migration routes and winter ranges in Central America are well documented (Chapman 1933, Wetmore 1965, Smith 1980). Migrating Turkey Vultures were observed in northwestern Colombia by Dugand (1947), Haffer (1959), and Olivares (1959), but there are no data on their abundance or ecology. Because seasonal changes in their abundance in Panamá have been observed, it is believed that the northern Lesser Yellow-headed Vultures are also migratory (Ridgley 1976).

A tight flock of at least 150 soaring Turkey Vultures was observed on 14 October 1978, some 16 km to the east of the town of Barranquilla, Colombia. Such an unusually large number suggested migrating birds. A closer view confirmed this; none of the vultures showed the whitish or dull yellow bands across the backs of their necks that characterize the resident race, *Cathartes aura ruficollis*. Although similar in general appearance and size to the Turkey Vulture, some birds of the flock had conspicuous orange-yellowish heads and dirty-whitish wing patches that identified them as Lesser Yellow-headed Vultures. The results presented here are based mainly on observations and line-transect counts made along the Caribbean coast between the ports of Barranquilla and Santa Marta in northern Colombia. They give a first account of the magnitude and ecological aspects of vulture migrations in South America.

Counts of vultures were made by driving along the Troncal del Caribe highway between Puente de la Barra, near the town of Cienaga, and Los Cocos, near the port of Barranquilla on the Magdalena River. This area includes most of Isla de Salamanca National Park. A detailed description of this region, including a portrayal of its flora and fauna, is found in Franky and Rodriguez (1976). Visibility along most of the highway was not impaired by vegetation, so nearly all roosting or soaring vultures could be counted within a broad corridor of up to more than 500 m on each side of the highway. Twenty-eight line transects, each covering a distance of 44 km, were made between 1000 and 1500 from 17 October 1978 to 17 January 1980. One person drove, holding the speed at a constant 70 km, while a second person, using a hand-operated counter, counted vultures with the naked eye. Due to similarities in their plumage coloration and silhouettes, Turkey Vultures and Lesser Yellow-headed Vultures, when soaring or roosting, were difficult to separate at a distance. Separate counts for resident Turkey Vultures and the race of migrating Turkey Vultures were even more difficult.

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TABLE 1. Date, relative abundance, and average number of vultures (*C. aura* and *C. burrovianus*) observed per line-transect count from 17 October 1978 to 17 January 1980.

Date	Number of individuals	Total/month	Number of counts	$\bar{x}$ individuals
17 Oct 1978	132	353	3	117.7
20 Oct 1978	137			
23 Oct 1979	84			
3 Nov 1978	210	741	4	185.3
4 Nov 1978	162			
15 Nov 1978	117			
26 Nov 1978	252			
7 Dec 1978	154	458	3	152.7
14 Dec 1978	165			
21 Dec 1978	139			
8 Jan 1979	174	266	2	133.0
17 Jan 1980	92			
16 Feb 1979	47	147	2	73.5
22 Feb 1979	100			
16 Mar 1979	39	39	1	39.0
24 Apr 1979	27	27	1	27.0
4 May 1979	19	35	2	17.5
15 May 1979	16			
3 Jun 1979	19	19	1	19.0
12 Jul 1979	24	45	2	22.5
20 Jul 1979	21			
2 Aug 1979	8	66	4	16.5
5 Aug 1979	19			
14 Aug 1979	24			
20 Aug 1979	15			
4 Sep 1979	83	223	3	74.3
18 Sep 1979	72			
26 Sep 1979	68			

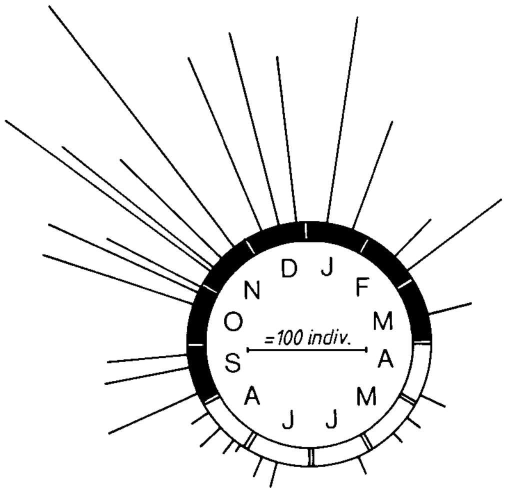

Fig. 1. Yearly distribution of relative abundances of *Cathartes* vultures in the study area, by months (J = January), from 28 line-transect counts 17 October 1978 to 17 January 1980). Black areas indicate migration period.

The characteristic yellowish nape of resident birds was visible only at close range and when birds were sitting or flying low. Because of these uncertainties, line-transect counts of resident and migrant Turkey Vultures and Lesser Yellow-headed Vultures made throughout the study were lumped into the single category of *Cathartes* vultures. The only other vulture of this genus, the Greater Yellow-head (*C. melambrotus*), is an Amazonian bird whose occurrence in the study area is highly unlikely.

The abundance of vultures varied seasonally, in accordance with the general migration pattern for nearctic migratory bird species (Table 1, Fig. 1). Thus, it is almost certain that flocks of Turkey Vultures observed along the Colombian Caribbean coast during the northern fall, winter, and spring seasons were migrating or wintering birds. In addition, Lesser Yellow-headed Vultures were observed in the study area in greater numbers during the migration period, often mixed in with the flocks of Turkey Vultures. Roughly, 1 Lesser Yellow-headed Vulture to every 5–10 Turkey Vultures was seen during the migration period, compared to a smaller proportion during the rest of the year. Therefore, it appears likely that migratory populations of *C. burrovianus* also wintered in the area.

Blake (1977 and pers. comm.) identifies migrating Turkey Vultures in Colombia, including the Santa Marta region, as belonging to the race *C. aura meridionalis*. Indeed, based on the known ranges of the races that could be possible migrants to the study area and on the measurements of a female specimen collected on 7 January 1979, the Turkey Vultures reported here as wintering birds may well have belonged to this race rather than to *C. aura septentrionalis*, as was assumed by Meyer de Schauensee (1964). The specimen, collected at Pozos Colorados, Santa Marta, was catalogued under Nr. IND-A-3186 at the collection of the Laboratorio de Investigacion de Fauna Silvestre, Div. de Fauna Terrestre, INDERENA, Bogota, D.E., Colombia. It measures as follows: wing length (flattened), 535 mm; tail length, 270 mm; tarsus, 63.5 mm; culmen (from cere), 24.5 mm; body weight, 1,420 g; ovary small, in nonreproductive state. The nominate race, *C. aura aura*, so far reported as a winter migrant only as far south as Panamá, and *C. aura jota*, essentially a highland bird not reported north of central Colombia, can both probably be ruled out as being involved in these migrations (Blake pers. comm.). With respect to the Lesser Yellow-headed Vultures that were observed to winter together with the Turkey Vultures, it seems reasonable to assign them to the nominate race *C. burrovianus burrovianus*, which ranges from southern México to Colombia. Previous records in northern

TABLE 2. Densities (individuals/km) of *Cathartes* vultures in the study area; 28 line-transect counts along 44 km of coast line each for a total of 1,232 km; 2,419 vultures counted.

Period	Number of counts	km	Number of individuals	Density
Migration	18	792	2,227	2.8
Nonmigration	10	440	192	0.4
Totals	28	1,232	2,419	($\bar{x}$ = 1.6)

South America for the larger *C. burrovianus urubutinga* include only April through October, suggesting migration from its southern range (Blake 1977). On 10 January 1979 a specimen soaring with a flock of five wintering Turkey Vultures was shot at the same place where the Turkey Vulture described above had previously been collected. It measured as follows: wing length (flattened), 495 mm; tail length, 255 mm; tarsus, 58.0 mm; culmen (from cere), 23.6 mm; body weight, 1,200 g; sex undetermined. Preservation of this specimen was not possible.

If the data from the line transects are subdivided into numbers of *Cathartes* vultures seen during the migration and nonmigration periods (according to the presence or absence of groups of 10 or more Turkey Vultures that soared or roosted together without obvious presence of food: black areas in Fig. 1), then the relative abundance of vultures observed during the migration period from September to March ($\bar{x}$ = 123.7 individuals per transect count) was significantly higher than during the nonmigration period from April to August ($\bar{x}$ = 19.2 individuals per transect count): $\hat{t} = 8.00 > 2.86 = t19$; $P \leq 0.01$. The density of *Cathartes* vultures, expressed as the number of individuals per kilometer of line transect, was seven times higher (2.8 individuals/km) during the migration period than during the nonmigration period (0.4 individuals/km) (Table 2).

According to Smith (1980), migrating Turkey Vultures in Panamá tend to abstain from food. In this study, however, Turkey Vultures that had arrived in great numbers were frequently observed feeding. Therefore, it may be inferred that they accepted this area as their winter home and did not extend their migration farther to the south. For several days after their arrival, flocks of 100 and more individuals were observed soaring and roosting jointly. Thereafter, these large flocks dissolved into smaller groups or single individuals. Especially when roosting in groups, wintering vultures took flight readily at the approach of an observer even when he was still 100–200 m away, while Turkey Vultures flushed during the nonmigration period, i.e. resident birds, usually took flight when an observer was at a distance of only 30–50 m. During the first observations in October 1978, the flocks of migrants roused in this way had a rather spectacular effect upon the local Black Vultures (*Coragyps atratus*). Soon after the first Turkey Vultures had begun to soar above their roosting place, Black Vultures came in from all sides. The speed of their flight and the way they flew in on a straight line to wheel about in the cloud of roused migrants suggested that they came to find carrion. On such an occasion on 17 October, several groups of two and three King Vultures (*Sarcoramphus papa*), almost never seen in this coastal area, were observed flying high above. Previous observations of the behavior of King, Black, and Turkey vultures feeding on carrion have shown (Koester and Koester-Stoewesand 1978) that Turkey Vultures in northern Colombia invariably are the first to appear at the carcass, attracting through their presence Black Vultures that in turn may lure King Vultures to the site. It seems possible, therefore, that the latter two species misinterpreted the unusually large flock of soaring migrants as an indication of the presence of food.

It seems generally accepted that migrants in the tropics harvest superabundant and/or sporadically available resources and are usually subordinate to the resident species (Karr 1976). This may apply only in part at the subspecies level, when one considers wintering versus resident Turkey Vultures. Although no detailed data on this subject were gathered, the amount of what appeared to be suitable food for the local Turkey Vultures did not seem to be more abundant during the wintering period compared to the rest of the year. Thus, if a relatively constant availability of food permitted a relatively stable population of *C. aura ruficollis* to exist in the study area, the presence of additional Turkey Vultures, *C. aura meridionalis*, with presumably similar feeding habits during the northern winter, should have resulted in a general food shortage and competition between these two races. Indeed, resident Turkey Vultures were never observed to share a carcass with their wintering conspecifics, which appeared to be more powerful flyers and generally stronger birds. In a remarkable contrast to the residents, migrants seemed to cope easily with the agressive feeding behavior of the Black Vultures. This was observed on 15 November 1978, when eight migrants and two Black Vultures fed on the carcass of a dog near the village of Tasajeras, Isla de Salamanca.

During the migration period, resident Turkey Vultures were more numerous in certain locations in which they had not been as frequently encountered during the rest of the year. At times, in Tayrona National Park to the east of Santa Marta, for example, the number of *C. aura ruficollis* nearly equaled the numbers of the common Black Vultures. It may be inferred from this that the wintering race displaced a certain percentage of the resident race to other habitats. Bent (1937) wrote that Turkey Vultures are effective in cleaning streets, garbage piles, and dump heaps in cities and are often seen feeding on the main highways in Florida where snakes, turtles, and small mammals have been killed by passing automobiles or where fish have been thrown away by fishermen. It is noteworthy that, in contrast to this statement, resident Turkey Vultures were virtually never seen feeding on garbage heaps and strictly avoided towns and cities where Black Vultures are abundant. But, like Turkey Vultures in Florida, *C. aura ruficollis* feeds on road kills and smaller carcasses along the highway in the study area. Compared to residents, therefore, wintering Turkey Vultures appeared to exploit a wider spectrum of food, as they were observed feeding on garbage near Cienaga as well as on road kills.

Seven times as many *Cathartes* vultures existed in the study area during the migration period as during the rest of the year (Table 2). Perhaps the exploitation of a wider range of food sources, comprising those fed upon by the local Turkey Vultures as well as those used by the local Black Vultures, enables wintering Turkey Vultures to coexist with both the resident race and the Black Vultures successfully. No such observations were possible in the case of the Lesser Yellow-headed Vultures. Throughout the year they were seen more frequently in the wetlands and mangrove swamps south and north of the Troncal del Caribe highway, where the majority of the birds believed to be wintering were observed.

The breeding seasons of the Black Vultures and Lesser Yellow-headed Vultures in the study area partly coincide with the migration period of Turkey and Lesser Yellow-headed vultures from the north. While more detailed information on season and breeding biology of the Black Vulture in the area is available (Koester and Koester-Stoewesand in press), our present knowledge of the breeding season of the Lesser Yellow-headed Vulture is limited to a single observation of an adult accompanied by two recently fledged young on 11 May 1979 in the mangrove swamps south of the Cienaga Grande de Santa Marta, known as the natural reserve area El Santuario. Nothing so far is known of the annual cycle of the resident Turkey Vultures and how their cycles might compare with those of the migrants. According to Smith (1980), however, Turkey Vultures in Panamá commence egg laying in February through early April. A similar timing of the breeding season for *C. aura ruficollis* in the study area is likely. Thus, during the northern winter, Turkey Vultures along the northern coast of Colombia are likely to be separated into breeding resident and nonbreeding wintering races.

A more extended ecological study of the relation of the migratory vultures with the residents treated herein and the resulting inter- and intraspecific competition for food and its possible effects on the breeding success of the residents should be of particular interest. Because vultures are large, conspicuous birds whose feeding habits can be studied without too much difficulty, studies of their behavior and ecology could contribute substantially to our present knowledge of the ecology of bird migration.

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The Northern Limit of the Hummingbird Genus *Oreotrochilus* in South America

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The hummingbird genus *Oreotrochilus* is represented by populations living at high altitudes in the South American Andes from north-central Ecuador to south-central Chile and adjacent Argentina (Berlioz and Jouanin 1942, Zimmer 1951, Peters 1945, Carpenter 1976, Olrog 1978). Ecuadorian populations constitute a morphologically distinct, allopatric taxon, which is related to the northern-most Peruvian and Bolivian species, *O. estella*, but is characterized by largely blue-headed adult males and is often treated as a separate species, *Oreotrochilus chimborazo* (Vuilleumier and Simberloff 1980, but see Zimmer 1951: 40). The northern-most of the three Ecuadorian *O. chimborazo* taxa is assigned to *O. c. jamesoni* (Jardine 1849), previously recorded in the western Cordillera as far north as Mt. Pichincha and in the eastern Cordillera as far north as the Guamani Pass, just north of Mt. Antisana (Orces 1944, Peters 1945, Corley-Smith 1969, Vuilleumier 1976). We here report a northward range extension of birds presumed to be of the *jamesoni* form, a presumption based upon two independent sets of visual observations in the headwaters of the Rio Pantavi, Imbabura Province, in the Mt. Cotacachi-Mt. Yana Urco de Piñán portion of the western range, about 70 km north of Mt. Pichincha (see Fig. 1).

Ortiz-Crespo visited the area on 22 December 1975 and saw a female *Oreotrochilus* feeding at the flowers of an isolated thicket of *Chuquiraga insignis* HB (Compositae) amid clumps of paramo grasses at an elevation of 3,600 m. A second visit to the area by Bleiweiss on 23 June 1980 documented the presence of a population, which was then tentatively assigned to *jamesoni*; at that time two records of adult males, both showing the all-blue head characteristic of the taxon *jamesoni*, as well as two of females, were made at elevations of 3,550–3,650 m in open or protected stream ravines where *Chuquiraga* was common.

In Ecuador, *Oreotrochilus* populations are found only above an elevation of 3,500 m up through the highest vegetated zones to the snow line. North of Mt. Pichincha, the western Andes are insular with respect to appropriate *Oreotrochilus* habitats. The deep, arid gorge cut by the Rio Guayllabamba effectively isolates Pichincha from the Cotacachi-Yana Urco massif to the north, which in turn is separated from the high mountains farther north by the course of the upper Rio Mira running roughly parallel to the Rio Guayllabamba and from high elevations to the east by an extension of the inter-Andean valley running north–south in northern Ecuador (see Fig. 1). Thus, in terms of both horizontal distance and ecological barriers, the range extension we record here is of biological significance.

These new records permit us to emphasize several facts about the biogeography of *Oreotrochilus* in general and of the Ecuadorian populations in particular. First, members of *Oreotrochilus* seem to occur in dry puna (cf. Vuilleumier and Simberloff 1980) or puna-like grassland habitat through much of their range. Our new record documents a paralleling between the distribution of *Oreotrochilus* and these habitats, because the Cotacachi-Yana Urco region is covered by dry, puna-like grassland. It should be pointed out, however, that *Oreotrochilus* apparently does occur in a variety of habitats, from dry, brushy slopes to wetter paramo, elsewhere in Ecuador (Vuilleumier 1967), so grassland habitat may not be a necessary condition for *Oreotrochilus* at its northern limits. Furthermore, the grasslands of Cotacachi-Yana Urco are frequently burned and heavily grazed by cattle throughout the year, and, therefore, it is difficult to say whether the presence of *Oreotrochilus* represents a recent invasion due to the creation of favorable conditions by man or is part of the historic pattern of differentiation of *O. chimborazo* in Ecuador. The presence of *O. c. jamesoni* at the Guamani Pass, the northern-most record for *Oreotrochilus* in the eastern Cordillera of Ecuador, has been suggested to result from the creation of favorable habitat due to human disturbance (Corley-Smith 1969). The Guamani Pass is an exceedingly wet site (Vuilleumier 1976), which might be unfavorable habitat for *Oreotrochilus* under natural conditions. Similarly, in the high-altitude regions immediately to the north of the presently revised western portion of the range, rainfall appears to be much greater than within the range (Ortiz-Crespo 1974). This additional correlation of *Oreotrochilus* distribution with climatic factors in western Ecuador, in light of the general ecology of the genus, suggests that *Oreotrochilus* is not a recent invader to the Cotacachi-Yana Urco region.

Also of interest is the co-occurrence of the plant *Chuquiraga* and *Oreotrochilus*. Ortiz-Crespo has never observed the birds feeding from plants other than *Chuquiraga insignis* in Ecuador, and the availability of this plant may be requisite for the presence of *Oreotrochilus* in the Ecuadorian part of its range. A high reliance of *Oreotrochilus* on *Chuquiraga* is corroborated by several other investigators. Corley-Smith (1969) also notes encountering *O. chimborazo* only in the presence of *Chuquiraga*, and Carpenter (1976) found, for some Peruvian populations of *O. estella*, an exclusive dependence on *Chuquiraga spi-*

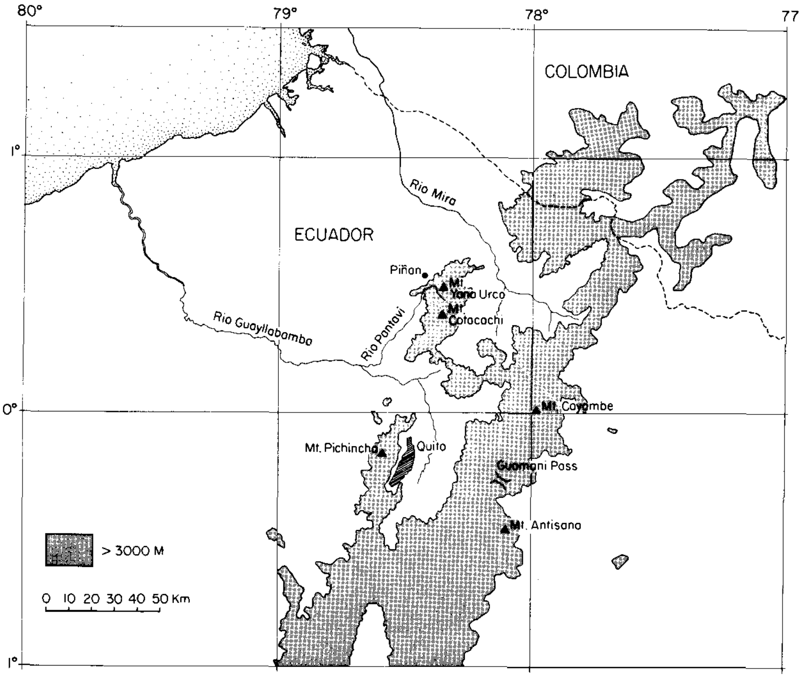

Fig. 1. Map of north-central Ecuador showing localities mentioned in the text.

noza as a native nectar source during the winter, nonbreeding season. Curiously, there are no *Oreotrochilus* records from Mt. Cayambe, the next major peak north of Mt. Antisana in the eastern Cordillera, although *Chuquiraga* occurs there (L. Holm-Nielson pers. comm. 1980). However, *Oreotrochilus* is also adapted in roosting, breeding, and other feeding habits to the vegetation and physiographic features of drier, high-altitude habitats (Carpenter 1976), and these factors may also influence distribution. The apparent absence of *Oreotrochilus* from the relatively undisturbed wet paramos of Mt. Cayambe may be due to these factors.

Our record of *Oreotrochilus* in the Cotacachi-Yana Urco area also points out a close parallel in the apparent northern terminus of this widespread genus with that of the Giant Hummingbird (*Patagona gigas*), another widespread species characteristic of the southern Andes. *Patagona* has previously been recorded on the Cotacachi-Yana Urco massif from the Lake Cuicocha area near Cotacachi (Ortiz-Crespo 1974), only 20 km south of our present record of *Oreotrochilus*. During Bleiweiss's visit, a single *P. gigas* was observed close to the *Oreotrochilus* populations, at 3,150 m on the west slope of Yana Urco, above Piñan, and the species was common east of this point on the west side of the inter-Andean valley. *P. gigas* differs ecologically from *Oreotrochilus*, occurring at lower elevations and in more xeric habitats, and the Guayllabamba canyon is apparently not a barrier for this species (Ortiz-Crespo 1974). Both occur in drier habitats, however, and may be similarly limited further northward by the increased rainfall in northernmost Ecuador.

There is no reason to believe that the currently revised northern limit of *Oreotrochilus* is definitive. The range extension we record here, however, highlights some of the major features in the geographical ecology of this Andean hummingbird.

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Differential Occurrence of Yearling and Adult Male Gadwalls in Pair Bonds

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Most age-specific information on breeding waterfowl has been concerned with the reproductive characteristics of females, and few data are available on the effects of age on male breeding biology. Weller (1964) and Lack (1968) have extensively reviewed the literature on breeding age in the Anatidae. Lack, in particular, noted that males of the Anatini, especially of the genus *Anas*, probably breed as yearlings. In the Athyini, a group in which a large excess of males compete for smaller numbers of females, drakes may not breed until the second breeding season. In the Mergini, most males take part in the breeding activities at the age of 3 (Lack 1968). As part of my research on the breeding ecology of the Gadwall (*Anas strepera*) in southern Manitoba, I obtained information on the age of paired males in order to evaluate the relationship of age to breeding acitivity.

During 1972–1975 at Delta and Marshy Point, Manitoba, I gathered data on 79 Gadwall pairs from observations following banding or directly from birds collected. All ducks were aged as yearlings (1 yr old) or adults (2 yr old or older) at the time of capture or collection (Blohm 1977).

In 39 cases, the ages of both pair members were known. Adult males were involved in 29 (74%) pair situations, while yearling males were involved in 10 (26%). In the 40 cases in which only the ages of males were available, adult drakes were present in 31 (78%) pair bonds, and yearling males were involved in the remaining 9 (22%). Adult male/adult female pairs (20 of 39, 51%) predominated over all possible sex-age combinations. Next in order of frequency were adult male/yearling female (9 of 39, 23%) and yearling male/yearling female (7 of 39, 18%) pair bonds. The most infrequent combination was the yearling male/adult female category (3 of 39, 8%).

The importance of the observed frequencies cannot be evaluated without a consideration of the relative availability of young and adult males during pairing. In southern Manitoba, I found that most Gadwalls arrived already paired, and Paulus (1980), working on the ecology of Gadwalls on their wintering grounds, stated that most birds were already paired upon departure from Louisiana during late March–early April. Although the age structure of the Gadwall on wintering areas is unknown and not readily determined, a conservative approach is to determine the proportion of yearling males present during the breeding season, using general population projection models (see Martin et al. 1979: 214). For example, I used the following values [e.g. see Anderson 1975, Mallard (*Anas platyrhynchos*); Blandin in prep., Black Duck (*Anas rubripes*)] as reasonable mean parameter estimates for a dabbling duck population:

S_{AM} = 0.60 = average annual survival rate for adult males;
S_{AF} = 0.55 = average annual survival rate for adult females;
S_{YM} = 0.45 = average annual survival rate for young males;
S_{YF} = 0.45 = average annual survival rate for young females;
R = 0.50 = sex ratio of young birds expressed as proportion male;
P = 2.0 = average annual recruitment rate or preseason age ratio (young/adult female in the fall population).

Accordingly, this modelling effort predicted a value of 0.40 as the asymptotic proportion of yearling males in a breeding-season population. Then, as-

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suming this value to be representative of Gadwalls in southern Manitoba, I evaluated the observed frequencies of males in pairing situations. In both samples the observed number of yearling males participating in pair bonds was significantly less than expected in a situation in which 40% of the breeding population was comprised of first-year drakes (one-tailed Binomial test: 10 of 39 pairs, $P < 0.05$; 9 of 40 pairs, $P < 0.02$, Snedecor and Cochran 1967).

The participation of a yearling or adult male in a pair bond is dependent upon several factors that influence courtship activity. Recent studies of the Anatini have indicated that first-year males may be less competitive during pair bonding due to plumage and behavioral immaturity. Stotts and Davis (1960) obtained information on 20 pairs of Black Ducks in Maryland and found no juvenile males in pair bonds during early pairing periods. This lack of participation in pairing was attributed to sexual immaturity in the first-year cohort (p. 132). McKinney (1965) found that plumage development and pairing occurred later in young captive Northern Shovelers (*Anas clypeata*) than among adults. In addition, young birds tended to be less competitive in mating situations. Definite differences between the displays of young and adult males were also documented in the Common Goldeneye (*Bucephala clangula*, Dane and Van der Kloot 1964) and, more recently, in the Gadwall (Kaltenhauser 1971) and the Wood Duck (*Aix sponsa*, Korschgen and Fredrickson 1976). Oring (1969) described differences in wing plumage between yearling and adult male Gadwalls. In addition, he suggested that yearling males were less likely to breed than adults and that some drakes did not attempt to mate.

In southern Manitoba, the observed frequencies suggest that age-related differences in neuroendocrine development, plumage growth, or courtship behavior may bestow a competitive advantage to older, more experienced males during early courtship, thereby explaining the preponderance of adult drakes selected by females in pair situations.

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Prey Handling in Yellow-crowned Night Herons

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Although an extensive literature exists on the foraging ecology of wading birds (reviewed by Kushlan 1978), detailed studies of the Yellow-crowned Night Heron (*Nyctanassa violacea*) are lacking. The yellow-crown is unique among the ardeids in that it specializes on crustacean prey (Palmer 1962, Hancock and Elliott 1978) and exhibits behavioral and morphological adaptations suited to this diet. Analyses of prey handling are presented here.

Feeding data were collected at Mount Sinai Harbor and John F. Kennedy Wildlife Sanctuary, Long Island, New York and Stone Harbor, New Jersey between May and August 1979 and 1980. Adult yellow-crowns were observed foraging in tide channels, tide-pool depressions, *Spartina* grass, and on mud flats. Prey included fiddler crabs (*Uca pugnax*), marsh crabs (*Sesarma reticulatum*), rock crabs (*Cancer irroratus*), and American eels (*Anguilla rostrata*). Data were also collected at a commercial shrimp farm situated on a cleared mangrove swamp in Chomes, Puntarenas Province, Costa Rica during October and December 1980. Yellow-crowns foraged in man-made basins containing penaeid shrimps, portunid crabs, and various fishes. All observations were made during daylight hours, although feeding also occurred at night.

Prey sizes were estimated by comparing captured large prey with the length of the heron's bill (mean bill length ± 1 SD = 72.7 mm ± 3.3, from measurements of 15 male and 15 female museum specimens, unpubl. data; dimensions of males and females were pooled, because sexes were indistinguishable in the field). Published data (Mulstay 1975) and measurements of prey remains from nest sites were used to estimate sizes of small prey. Prey-handling times were recorded with a stopwatch. (I defined prey-handling time as the time elapsed between initial grasping of prey and swallowing.)

Handling time varied directly with prey size within Brachyura (Fig. 1). A Model I regression of logarithmically transformed handling times on rank order of crabs by increasing size (1 through 4) was highly significant ($0.001 < P < 0.005$; regression equation: $y = 0.611x + 0.165$; Sokal and Rohlf 1969), justifying the above conclusion. All observations were pooled within a given prey category regardless of geographic locality. Crabs exhibited no marked behavioral differences among species after capture; therefore, size was considered the major determinant of handling time. There was a direct association between handling time and prey length within *Anguilla rostrata* (Fig. 2, Kendall Tau coefficient = 0.566; $0.008 < P < 0.014$; Gibbons 1976). Typically, all eel size classes wrapped their body around the yellow-crown's bill during manipulation, contributing to

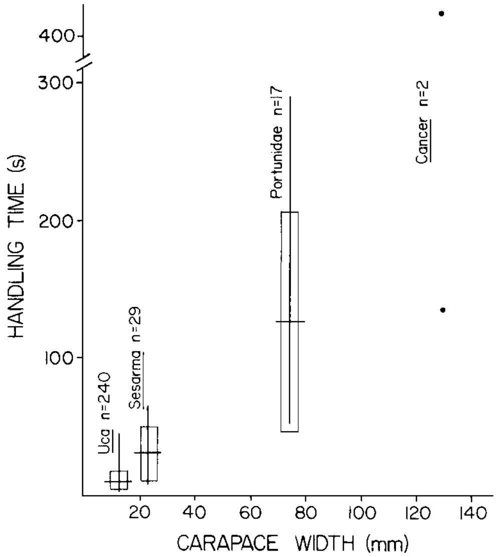

Fig. 1. Handling time of Yellow-crowned Night Herons in relation to prey size within Brachyura. Horizontal lines represent means, vertical lines depict ranges, rectangles enclose mean ± 1 SD, and points indicate individual observations.

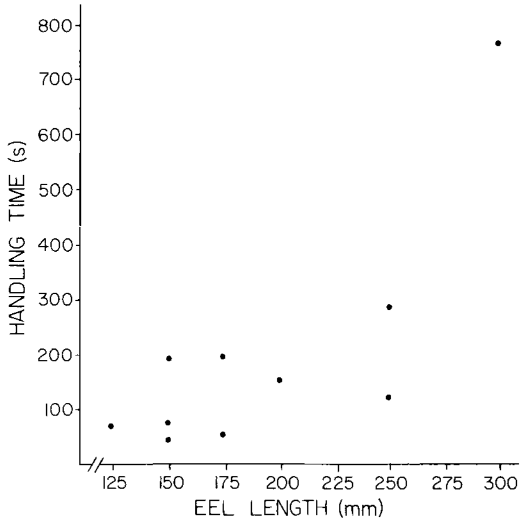

Fig. 2. Handling time of Yellow-crowned Night Herons in relation to prey length within *Anguilla rostrata*. Points represent individual observations.

TABLE 1. Frequencies of prey dropping by Yellow-crowned Night Herons.[a]

Prey	Mean carapace width (mm)[b]	Prey (n)	Drops/prey	Percentage of prey dropped ≥1 time
Uca pugnax	13.2	240	0.10	7.5
Sesarma reticulatum	22.7	29	0.90	31.0
Portunidae	75.0	17	4.24	82.4
Cancer irroratus	130.0	2	9.00	100.0

[a] Data are from field observations in New York and New Jersey, except for Portunidae (not identified to genus), which were observed in Chomes, Puntarenas Province, Costa Rica.

[b] Mean sizes of Portunidae and *Cancer* were estimated in the field (see text). The mean size of *Uca* was determined from 17 carapaces found in prey remains at nest sites. The mean size of *Sesarma* was determined from measurements of 248 individuals from Mount Sinai Harbor, New York (Mulstay 1975).

handling time. Eels also demonstrate this behavior when handled by other ardeids (Recher and Recher 1968). Amphipods and small fishes (<20 mm) constituted the category of smallest prey captured by yellow-crowns during my field observations. Consumption of these prey occurred almost instantaneously after grasping.

The frequency of prey (crab) dropping during manipulation is reported in Table 1 (an item that fell from the bill while the heron's head was raised was considered a "drop"). Larger crabs were dropped more frequently than smaller ones (R×C test of independence; $G = 60.34$, $df = 3$, $P < 0.005$; Sokal and Rohlf 1969). Yellow-crowns transported greater than 95% of larger prey, including rock crabs, portunid crabs, large marsh crabs, and eels, away from submerged areas to exposed terrestrial patches. Smaller prey (fiddler crabs and small fishes) were rarely carried to other sites before ingestion. The transport of prey to exposed surfaces is common among wading birds (Kushlan 1978) and is obviously a measure associated with reducing escapes (Recher and Recher 1968). Prey transported by yellow-crowns moved awkwardly on exposed surfaces and failed to escape when dropped. The herons usually impaled these prey repeatedly with their bills by jabbing their heads downward. Herons removed the crabs' chelae and legs by gripping either the appendages or carapaces in their bills and then vigorously shaking their heads. The carapaces were crushed between the mandibles and swallowed with characteristic upward head tilting; the appendages were eaten subsequently. After the entire prey was consumed, the heron returned to the water and drank to facilitate swallowing.

In summary, the duration of prey handling by Yellow-crowned Night Herons is directly related to prey size. This relationship has been found in other wading birds (Recher and Recher 1968, Kushlan 1979, Quinney and Smith 1980). Prey transport by yellow-crowns away from submerged areas to exposed surfaces is a behavior used to reduce prey escapes during manipulation.

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Synchronous Fluctuations in Christmas Bird Counts of Common Redpolls and Piñon Jays

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Bock and Lepthien (1976) described synchronous southward eruptions of eight North American boreal seed-eating bird species, based upon an analysis of Christmas Bird Count (CBC) data. These findings were confirmed by an analysis of banding data for two of the species—Common Redpoll (*Carduelis flammea*) and Purple Finch (*Carpodacus purpureus;* Kennard 1976, 1977). Between 1962 and 1971, synchronous eruptions of the eight species occurred in the winters of 1963–1964, 1965–1966, 1968–1969, 1969–1970, and 1971–1972. Available evidence suggests that these eruptions were triggered by widespread seed-crop reductions among high-latitude tree species—especially spruce (*Picea*) and birch (*Betula*). Inspection of our 1962–1971 CBC data bank indicated that only the Piñon Jay (*Gymnorhinus cyanocephalus*) among 616 additional species fluctuated in a manner strongly resembling that of the boreal birds.

In Table 1, mean numbers of Piñon Jays counted per party-hour over the 10-yr period for which I have computerized CBC data are compared to the equivalent numbers of Common Redpolls—the species that showed the boreal-bird eruption pattern most strongly (Bock and Lepthien 1976). The Pearson product-moment correlation between jay and redpoll numbers was 0.908 ($P \cong 0.0003$); the nonparametric Spearman rank correlation for the two data sets was 0.720 ($P \cong 0.01$).

Piñon pines (*Pinus edulis* and *P. monophylla*) produce sporadically abundant cone crops, and Piñon Jays are known to move opportunistically in search of them (Balda and Bateman 1972, Ligon 1978, Forcella 1980). If Piñon Jays "erupted" in the high years 1963–1964, 1965–1966, 1968–1969, 1969–1970, and 1971–1972 (Table 1), then they should have been detected on more CBC's in those 5 yr than in the other 5. I tested this by determining the number of counts in each year that reported at least one Piñon Jay, adjusting these data to 1962 levels to compensate for the overall increase in CBC's each successive year. Results showed that Piñon Jays were detected on significantly more counts in eruption years ($\bar{x} = 17.6$, SD = 2.06) than in noneruption years ($\bar{x} = 13.0$, SD = 3.86; $t = 2.34$, $P < 0.05$).

TABLE 1. Mean number of Common Redpolls and Piñon Jays counted per party-hour per year on mainland U.S. and Canadian Christmas Bird Counts between 1962–1963 and 1971–1972 (n = 8,129).

Year (fall)	Common Redpolls	Piñon Jays
1962	0.82	0.09
1963	2.48	0.29
1964	0.40	0.15
1965	3.03	0.35
1966	0.28	0.09
1967	0.23	0.13
1968	3.42	0.33
1969	3.57	0.28
1970	0.15	0.15
1971	2.55	0.22

One interpretation of these results is that some common environmental factor affected movements and/or population sizes of the two species between 1962 and 1971. Because both species are dependent upon irregularly available tree seeds, it is tempting to speculate that piñon pine cone crops fluctuated in synchrony with seed crops of more boreal tree species during this period.

Results of this study also could be due to some artifact of CBC data, but Piñon Jays and Common Redpolls concentrate in winter in very different parts of North America, and it does not seem possible that CBC observers could be influencing one another between these regions. Certain nationwide weather patterns might be influencing both CBC observers and the birds, but this should have resulted in synchrony between redpoll numbers and counts of a great many species. No such pattern is apparent in CBC data.

The synchrony in fluctuations of redpoll and Piñon Jay numbers could be due to chance, but it is very difficult to calculate such a probability exactly because of the small sample size involved ($n = 10$). Spearman rank correlation almost certainly is an unrealistically conservative estimate in the present case ($P \cong 0.01$), because it gives much weight to rank differences between pairs of values that actually differ very little in their absolute positions in the two data sets (Table 1). Neither variable differs significantly from a normal distribution, so use of the parametric r is justified ($P \cong 0.0003$). Small sample size, however, makes tests for normality comparatively weak.

There are 616 species in our CBC data bank not considered to be boreal tree-seed-eating birds. It seems probable that one or two would show such a strong correlation with redpoll numbers by chance alone. The probability that it would occur by chance between redpolls and another notoriously vagrant tree-seed predator seems very slight, although such a possibility cannot be be discounted. If the relationship between jays and redpolls is real, and if it is due to fluctuations of their food supplies, the relationship suggests that geographic and interspecific synchrony among tree-seed crops may be much more widespread than previously suspected.

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Mortality of Duckling Attributed to Separation from Mother and Subsequent Protracted Exposure to Low Ambient Temperature

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On 17 May 1981 I was observing the breeding behavior of dabbling ducks on the St. Lawrence River near Lancaster, Ontario. A female Mallard (*Anas platyrhynchos*) and her nine 1–2-day-old ducklings were feeding as they slowly moved along the marshy edge of St. Francis Island. At 1130, when they reached the point closest to Hamiltons Island (ca. 0.3 km away), the female called and swam into open water, followed by eight of the ducklings. The ducklings clustered together and stayed within 1 m of the female during the entire crossing; the female called frequently and kept her head close to her body. The shoreline where the female reached Hamiltons Island was rocky; to the south the shore remained rocky, but a cattail marsh was approximately 300 m to the north. The female (followed closely by the brood) swam to within 5 m of shore and then followed the shore to the marsh. She took the brood to shore, where I lost sight of them.

The ninth duckling left St. Francis Island at the same place about 5 min after the others and remained about 100 m behind them. It presumably saw the others depart, because it followed the same trajectory. The wind was blowing at 12–15 km/h from the northwest and 0.5-m-high waves of short interval buffetted the duckling. It reached Hamiltons Island about 8–10 min after the others; by this time, however, the brood presumably was out of sight of the lone duckling. It stayed there approximately 45 min but then swam to about 30 m offshore. It remained there in water 2 m deep, swimming in circles with its head continually dipping down. Within 60 min of separation from the female, it was dead.

Temperatures on this day were the lowest since 1944, and that night they were 0°C or below. Nighttime temperatures had dipped to 2°C for the two nights before this incident, and they were to 0°C for the two nights thereafter; wind velocity reached a steady 35–40 km/h the day after. When I first saw the brood, air temperature under bright sun was approximately 4°C and water temperature was approximately 3°C. This duckling appeared healthy and was dry when retrieved. It swam strongly, despite the wind from the northwest and a 10–12 km/h current flowing north between the two islands; it reached the island at exactly the same location as the female. Presumably the duckling was cold and could have conserved or even gained body heat had it gone to shore and sat on the stones in the sun. Periodic brooding by the female could potentially have provided an additional source of heat, which may have been why she took the young to shore as soon as she reached the marsh. The relatively short (about 5 min), but critically timed, separation from the female was apparently enough for the duckling to become lost and subsequently to succumb to exposure.

Dabbling ducks in this habitat nest on islands and move their newly hatched broods to marshy areas associated with islands. They frequently move broods between islands, presumably to new feeding areas. Movements of up to 2 km are common in Mallards, Black Ducks (*A. rubripes*), American Wigeon

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(*A. americana*), and Gadwall (*A. strepera*). There is considerable potential for ducklings to become separated from their mothers. Risk of exposure to adverse climatic conditions is great, especially early in the year when cold water and cold air often combine with rain and high wind. In addition, females that nest early in the season always risk having broods hatch when food is scarce or unavailable. This female must have begun egg laying during the first week of April, during an unusually mild early spring but cool and wet late spring. This incident is significant because it emphasizes the hazards associated with the timing of nesting for females and the consequences of even a brief lapse of attentiveness by young and/or females.

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Rockhopper Penquin (*Eudyptes chrysocome*) Record at Palmer Station, Antarctica

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An adult male Rockhopper Penquin (*Eudyptes chrysocome*) with a broken wing was collected on Cormorant Island near Palmer Station, off the south coast of Anvers Island, Antarctic Penninsula (64°8'S, 63°58'W) on 29 December 1980. The specimen is deposited at the Academy of Natural Sciences of Philadelphia (uncatalogued). This locality is approximately 1,100 km from the nearest breeding area of the species, the islands off Cape Horn. The bird was standing at the edge of a colony of nesting Adelie Penguins and appeared alert and in good condition except for its injury. Dissection and weighing produced the following wet weights: total, 2,532 g; pectoral muscles, 440.44 g; thigh muscles, 219.62 g; liver, 76.86 g; heart, 28.14 g; brain, 10.91 g; stomach, 18.45 g; the stomach was empty and there were no visible subcutaneous fat deposits. Both testes were present; they were 180 mm by 80 mm in length and width and, together, weighed 1.23 g. Color notes were made from life. The eyes were dull red, the feet whitish pink with black soles, and the bill reddish brown.

Male Rockhopper body weights on Macquarie Island average 2.7 kg (range, 2.1–3.2) (Warham 1963); the individual collected near Palmer Station was therefore well within the expected weight range. Unless this individual was taken onboard ship, transported, and then released, it most likely came from the Falkland Islands (G. E. Watson pers. comm.), where Rockhoppers breed abundantly (Pettingill 1960, Strange 1965). The facial characteristics and head plumes were consistent with the dark-faced form (*chrysocome*) expected for a bird from South America or the Falkland Islands (Carins 1974), although the underwing pattern was more like that of the subtropical form *moseleyi* (Prevost and Moughlin 1970).

The peak egg-laying date for Rockhoppers on the Falkland Islands is estimated to be 20 November (Warham 1972). If this individual were breeding, he might have recently been relieved by his mate (males usually incubate first, for approximately 25 days) and gone out to sea to feed, which would explain his occurrence far from the Falkland Islands. A broken wing might well have hindered his ability to return to the Falklands. This is the first record for this species at Palmer Station (confirmed by D. Parmelee).

I am grateful to P. Tirrell, who first spotted the Rockhopper. I also wish to thank (in alphabetical order) R. Fraser, D. Murrish, D. Parmelee, P. Peitz, and D. Wiggin. R. E. Ricklefs and G. E. Watson provided critical comments on the manuscript. This specimen was collected during research supported by the U.S. Antarctic Research Program under grant number DPP-79-08570 awarded to R. E. Ricklefs, University of Pennsylvania.

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Received 13 July 1981, accepted 4 November 1981.

Distribution of the Quetzal in Honduras

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I studied the Quetzal (*Pharomachrus mocinno*) on behalf of the Department of Wildlife and Environmental Resources, Honduras from October 1977 to November 1980, in part to determine its nationwide distribution. Quetzals were reported from the following mountains by American Peace Corps volunteers who responded to a questionnaire regarding the distribution of the species (numbers are those used in Fig. 1). The questionnaire requested rural-living volunteers to interview residents of the locality regarding the presence of Quetzals. These residents are very knowledgeable concerning the species of wildlife present.

The locations of the mountains are indicated in Fig. 1 by number. *Ocotepeque:* (1) Montaña Montecristo; *Yoro:* (2) Montaña de Pijol, (3) Montaña de Yoro; *Intibuca:* (4) Montaña Pacayas, (5) Montaña Pamina; *Cortes:* (6) Montaña Cusuco, (7) Montaña San Ildefanso; *El Paraiso:* (8) Montaña Yuscaran; *Francisco Morazan:* (9) Montaña La Tigra, (10) Montaña El Chile, (11) Montaña de la Flor, (12) Montaña de Uyuca; *Copan:* (13) Montaña San Jose and/or Montaña San Antonia; *Olancho:* (14) Sierra de Algalta, (15) Montaña de Almendares; *Lempira:* (16) Montaña de Celaque; *Altantida:* (17) Montaña Pico Bonito. The following Quetzal locations also were reported, but no literature or map reference to them could be found either in Honduras or in the United States. *Santa Barbara:* Montaña Paso Viejo; *El Paraiso:* Montaña Jogon; *Francisco Morazan:* Montaña de Palo Alto. This could reflect local names for the mountains.

The above are additional Quetzal locations to those reported by Monroe (1968). He listed the following. *Santa Barbara:* (18) Montaña Santa Barbara; *Ocotepeque:* (19) Montaña El Chorro; *Francisco Morazan:* (20) Montaña Monsettat; *Lempira:* (21) Montaña de Puca; *La Paz:* (22) Montaña La Cruz; *Comayagua:* (23) mountains south and east of the plain of Comayagua.

Appreciation is expressed to former Peace Corps volunteers in Honduras for assistance in supplying distributional information.

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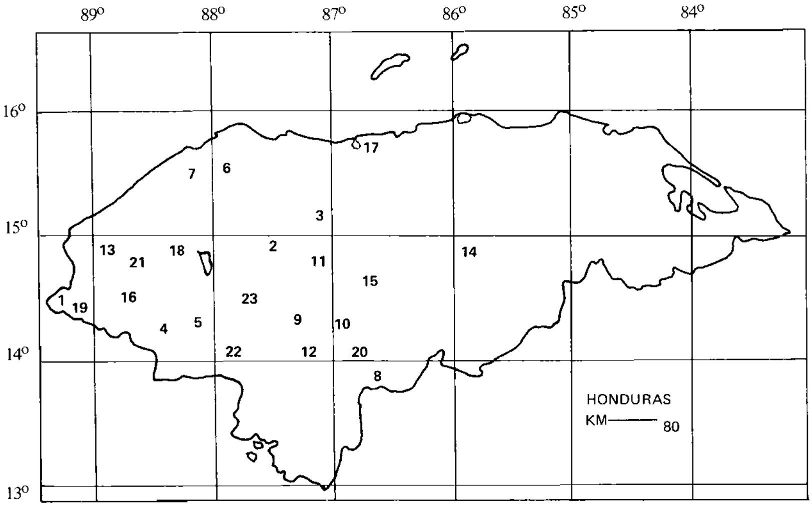

Fig. 1. Map of Honduras showing the distribution of the Quetzal. Map locations are coded in the text.

COMMENTARY

Macaroni Penguins: Comment on Mistaken King George Island Breeding Record and Southerly Range Extension

NICHOLAS J. VOLKMAN,[1] WAYNE Z. TRIVELPIECE,[1] NEIL P. BERNSTEIN,[2] AND PAUL C. TIRRELL[3]

On the basis of a personal communication from Polish researchers at Arctowski Station, Point Thomas, Admiralty Bay, King George Island (62°10′S, 58°30′W), Bernstein and Tirrell (1981) stated that for the first time a few Macaroni Penguins (*Eudyptes chrysolophus*) bred on King George Island during the 1979–1980 austral summer. Bernstein and Tirrell further suggested that Macaroni Penguin populations might be increasing in the area of the Antarctic Peninsula. Volkman and Trivelpiece have communicated several inaccuracies in Bernstein and Tirrell's paper, and we wish jointly to correct these errors.

Volkman and Trivelpiece did research on pygoscelid penguins at Pt. Thomas during the austral summers of 1976–1977, 1977–1978, and 1980–1981 and saw no evidence of breeding Macaroni Penguins. Furthermore, B. Jablonski (pers. comm.), a Polish ornithologist who studied penguins at Pt. Thomas during the austral summers of 1978–1979, 1979–1980, and 1980–1981, did not observe any breeding Macaroni Penguins. On several occasions, however, Volkman and Trivelpiece have seen molting Macaroni Penguins late in the season. For whatever reason, the personal communication to Bernstein and Tirrell of breeding Macaroni Penguins at Pt. Thomas appears to be inaccurate.

Even if this record of breeding Macaroni Penguins were verifiable, Bernstein and Tirrell's contention that it represents a southward extension of their range was erroneous. Breeding Macaroni Penguins have been reported on Nelson Island (Andersson 1905, Watson et. al. 1971), Gibbs Island (Watson et al. 1971), Deception Island (62°57′S; not 58°S as in Bernstein and Tirrell 1981) (Gain 1914, Watson et al. 1971), and Livingston Island (J. Croxall, pers. comm.), all of which are south of King George Island. In addition, Watson collected a Macaroni Penguin 10 km north of Palmer Station on Dream Island (G. Watson, pers. comm.).

We wish to thank J. P. Croxall for his communication and G. E. Watson for his suggestions and criticisms.

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Fellows and Elective Members are reminded that **nominations for Elective Members** may be submitted to the Secretary on the prescribed form up until five months prior to the opening of the next Stated Meeting. The deadline for 1982 is **10 May. Nominations for Fellow** of the A.O.U. also must be received by that date. Nominations for President-Elect, Vice President and three Elective Councilors may be made in writing to the Secretary at any time prior to the Annual Meeting.

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The sixth annual meeting of the **Colonial Waterbird Group** will be held 4–7 November 1982 in Washington, D.C. A symposium on the feeding biology of waterbirds is planned. Papers given at the meeting are eligible, after refereeing, for publication in *Colonial Waterbirds.* Anyone wishing to contribute to either the symposium (deadline **1 September**) or general session (deadline **15 September**) should contact **Dr. Michael Erwin, U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland 20708.** Information concerning registration can also be obtained from Dr. Erwin.

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The AOU Student Awards Committee issues the following reminders to all students interested in competing for the AOU Student Paper Award and the two Nellie Johnson Baroody Student Paper Awards at the 1982 AOU meetings: (1) To qualify for the competition, each student must submit an expanded abstract of the paper directly to the chairperson of the AOU Student Awards Committee (**Douglas Mock, Department of Zoology, University of Oklahoma, Norman, Oklahoma 73069**) by the "Call for Papers" deadline in the meeting announcement. (2) Appropriate applications with expanded abstracts must be submitted separately for the student paper awards and for the Marcia Brady Tucker travel awards. (3) A student is ineligible for student paper awards if she/he shares authorship of a paper, i.e. the student must be the exclusive author.

The American Ornithologists' Union will hold its annual meeting in Chicago, Illinois from **10–14 October 1982.** A formal call for papers is enclosed with this issue of *The Auk,* with a deadline for submission of abstracts for papers and poster sessions of **20 May 1982.** For further information on the scientific program, contact **James R. Karr, Program Chairman, Department of Ecology, Ethology, and Evolution, University of Illinois, 606 E. Healey, Champaign, Illinois 61820 USA.**

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REVIEWERS FOR THE AUK, 1980–1981

The Auk is fortunate to benefit from the services of many individuals who act as reviewers of manuscripts that are submitted. Their efforts are considerable, and their care and constructiveness continue to impress me as an Editor and as a sometime author. The individuals listed below helped make publication of a journal with high scientific and scholarly standards possible; my thanks to all of them.

Individuals who have contributed reviews of two or more manuscripts are indicated by an asterisk.

Ian Abbott, David G. Ainley, John Alcock*, Thomas Alerstam, Dean Amadon, Daniel W. Anderson, Ted R. Anderson, C. Davison Ankney, Einar Arnason, John C. Avise, Robert O. Bailey, Allan Baker, Myron C. Baker, Robert J. Baker, George S. Bakken, Russell P. Balda, Thomas G. Balgooyen*, David F. Balph, Martha Balph*, Richard C. Banks*, Luis F. Baptista*, George F. Barrowclough*, George A. Bartholomew, Jr., Thomas S. Baskett, Range Bayer*, Jeff Baylis, Michael Beecher*, Colin Beer*, Marc Bekoff, Frank C. Bellrose, Jr.*, Louis B. Best*, T. R. Birkhead, Charles R. Blem, Peter Boag, Walter Bock*, William R. P. Bourne, John H. Brackenbury, Richard A. Bradley*, Eliot Brenowitz, I. Lehr Brisbin*, Pierce Brodkorb*, Richard G. B. Brown*, Charles J. Burke, M. Byrd, William A. Calder, Jr.*, Thomas Caraco, Cynthia Carey*, Lynn F. Carpenter, Susan M. Case, Graeme Caughley, Mary H. Clench, Charles T. Collins*, Michael Collopy, Edward F. Connor, Peter G. Connors, Michael R. Conover*, Fred Cooke, John Cooper, Kendall W. Corbin, Richard Cowie, Joel Cracraft*, Robert B. Craig, Richard D. Crawford, John Croxall, E. Curio, Thomas W. Custer, John Davis, David DeSante, Diane De Steven, Robert W. Dickerman, James J. Dinsmore, David S. Dobkin, Richard A. Dolbeer, Hilary Dow, R. D. Drobney, William H. Drury, Alfred M. Dufty, Jr., Arthur E. Dunham, Erica H. Dunn*, Thomas J. Dwyer*, Eugene Eisenmann, Phillip F. Elliott, John T. Emlen, Robert Epting, Anthony J. Erskine, R. Michael Erwin*, P. G. H. Evans, Roger M. Evans*, David Ewert, C. J. Feare*, J. Alan Feduccia, Peter Feinsinger, Millicent Ficken*, James S. Findley, Hans Fisher, Walter Fitch, John W. Fitzpatrick*, Brian K. Follett, Eric D. Forsman*, W. J. Francis, Leigh Fredrickson, Herbert Friedmann, Carl Gans, C. Lee Gass*, A. J. Gaston, Sidney A. Gauthreaux, W. George, Frank B. Gill*, Robert E. Gill, P. D. Gingerich, Bradley M. Gottfried, Gilbert Gottlieb, Walter D. Graul, Russell Greenberg, Paul J. Greenwood, T. C. Grubb, Jr., Joseph A. Grzybowski, Svein Haftorn, Caldwell D. Hahn, F. Reed Hainsworth, William J. Hamilton, III, M. P. Harris, Richard J. Harris, Jeremy J. Hatch, Helen Hays, Robert E. Hegner, Dennis Heinemann*, Carl W. Helms*, Charles J. Henny*, Wayne Hoffman*, A. J. Hogan-Warburg, Richard T. Holmes, Dominique G. Homberger, John L. Hoogland*, Henry F. Howe*, Donald F. Hoyt*, John P. Hubbard, George L. Hunt, Jr.*, R. Hutton, Jerome A. Jackson*, Frances C. James*, Daniel H. Janzen*, Olli Järvinen*, Joseph R. Jehl, Jr.*, Paul A. Johnsgard*, Douglas H. Johnson*, David W. Johnston, Richard F. Johnston*, James R. Karr*, Janet Kear, J. Allen Keast, Bretton W. Kent, Paul Kerlinger, Lloyd F. Kiff, Lawrence Kilham, James R. King*, Warren B. King, Erwin E. Klaas*, Richard W. Knapton, Carl E. Korschgen, Gary Krapu*, John R. Krebs,Donald E. Kroodsma, James A. Kushlan, Mary K. LeCroy, Louis Lefebvre, Ross Lein*, Robert E. Lemon*, K. Lessells, J. David Ligon*, C. D. Littlefield*, Clare S. Lloyd, William J. Mader, Chris Marsh, Carl D. Marti*, Dennis J. Martin, Elden W. Martin, L. D. Martin*, Steven Martindale, Barbara W. Massey, Harold F. Mayfield*, Donald A. McCrimmon, Jr., Christopher McGowan, Judith W. McIntyre, Ann McNabb, A. H. Meier, Charles Meslow, L. Richard Mewaldt, David Miller*, Don E. Miller*, Douglas W.

(continued on p. 315)

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An **International Symposium on the Tamaulipan Biotic Province** will be held at La Quinta Royale Motor Inn, Corpus Christi, Texas, on **28–30 October 1982.** The symposium will emphasize all ecological aspects of the biome: vegetation, invertebrates, vertebrates, ecological structure and function, biological resources (use and effects), and management. Abstracts of contributed papers are due 1 August 1982; abstracts for invited papers must be received by 1 September 1982. For information on the program, contact **Gene W. Blacklock, Curator, Welder Wildlife Foundation, P.O. Drawer 1400, Sinton, Texas 78387** or **David Riskind, Head, Resource Management Section, Texas Parks and Wildlife Department, 4200 Smith School Road, Austin, Texas 78744.** For information on registration, contact **Jimmie R. Picquet, Director, John E. Conner Museum, Texas A&I University, P.O. Box 2172, Kingsville, Texas 78363.**

The joint **8th International Conference on Bird Census Work** and the **6th Meeting of the European Ornithological Atlas Committee** will be held at Newland Park College, Chalfont St. Giles, Buckinghamshire, United Kingdom, on **5–9 September 1983.** The conference will include papers on validation and testing of census methods, application of census techniques to bird community studies within and between habitats, description of vegetation and habitats for use in ornithological studies, atlas studies, and data processing methods. For further information, contact **R. J. Fuller, British Trust for Ornithology, Beech Grove, Tring, Hertfordshire, HP23 5NR, United Kingdom.**

COMMENTARY

Macaroni Penguins: Comment on Mistaken King George Island Breeding Record and Southerly Range Extension

NICHOLAS J. VOLKMAN,[1] WAYNE Z. TRIVELPIECE,[1] NEIL P. BERNSTEIN,[2]
AND PAUL C. TIRRELL[3]

On the basis of a personal communication from Polish researchers at Arctowski Station, Point Thomas, Admiralty Bay, King George Island (62°10′S, 58°30′W), Bernstein and Tirrell (1981) stated that for the first time a few Macaroni Penguins (*Eudyptes chrysolophus*) bred on King George Island during the 1979–1980 austral summer. Bernstein and Tirrell further suggested that Macaroni Penguin populations might be increasing in the area of the Antarctic Peninsula. Volkman and Trivelpiece have communicated several inaccuracies in Bernstein and Tirrell's paper, and we wish jointly to correct these errors.

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We wish to thank J. P. Croxall for his communication and G. E. Watson for his suggestions and criticisms.

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Fellows and Elective Members are reminded that **nominations for Elective Members** may be submitted to the Secretary on the prescribed form up until five months prior to the opening of the next Stated Meeting. The deadline for 1982 is **10 May. Nominations for Fellow** of the A.O.U. also must be received by that date. Nominations for President-Elect, Vice President and three Elective Councilors may be made in writing to the Secretary at any time prior to the Annual Meeting.