



Experimental Brood Manipulations and the Monoparental Threshold in Snail Kites

Steven R. Beissinger

The American Naturalist, Vol. 136, No. 1. (Jul., 1990), pp. 20-38.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0147%28199007%29136%3A1%3C20%3AEBMATM%3E2.0.CO%3B2-7>

The American Naturalist is currently published by The University of Chicago Press.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ucpress.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

EXPERIMENTAL BROOD MANIPULATIONS AND THE MONOPARENTAL THRESHOLD IN SNAIL KITES

STEVEN R. BEISSINGER

School of Forestry and Environmental Studies, Yale University, 205 Prospect Street,
New Haven, Connecticut 06511, and Department of Zoological Research,
National Zoological Park, Washington, D.C. 20008

Submitted August 29, 1988; Revised March 3 and June 14, 1989; Accepted October 16, 1989

Parental care may require substantial investments of time and energy (Drent and Daan 1980; Walsberg 1983; Thompson and Nichol 1986). A parent must choose between continuing to invest reproductive effort in a breeding bout or deserting to begin a second reproductive attempt considering the costs and benefits involved, including the probability of reproductive success for each attempt (Trivers 1972; Dawkins and Carlisle 1976; Boucher 1977; Maynard Smith 1977; Alexander and Borgia 1979; Beissinger 1987*b*). Clutch or brood size represents the expected benefit of reproduction and is also related to the costs (Drent and Daan 1980; Beissinger 1987*b*). Clutch or brood size may also be considered a life-history trait coadapted (in the sense of Stearns 1976) with male and female patterns of parental care (Walters 1982; Beissinger 1986).

The effect of brood size on parental-care patterns may best be evaluated in species with flexible mating systems, in which one or both sexes have options of obtaining other mates and reproducing again during a breeding season (see, e.g., Lack 1968; Davies and Lundberg 1984; Persson and Öhrstrom 1989). Such a mating system occurs in the snail kite (*Rostrhamus sociabilis*; Beissinger and Snyder 1987), a Neotropical hawk that feeds primarily on freshwater snails (Haverschmidt 1962; Beissinger 1988). Mate desertion in the Florida snail kite is facultative (Beissinger and Snyder 1987): a female or male may abandon its mate and renege with another one (sequential polyandry or polygyny) while its first partner finishes rearing the young alone for 3–5 additional weeks, or both mates may care for the young until they become independent (monogamy). Offspring mortality, however, occurs at only 4% of nests after mate desertion (Beissinger and Snyder 1987).

Several proximate factors affect the occurrence and timing of mate desertion by kites in Florida (Beissinger and Snyder 1987). First, the occurrence of desertion is negatively correlated with distances traveled from nests in search of snails, suggesting that the probability of mate desertion at a given nest is positively related to food supply. Since larger broods of kites require more food and greater food-delivery rates than smaller broods, the food supply required to meet the

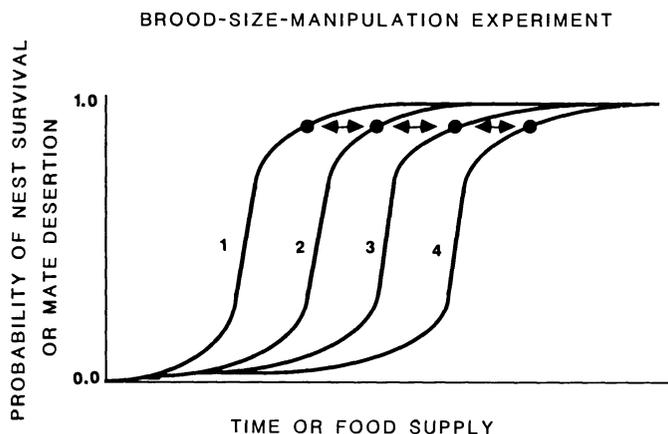


FIG. 1.—Threshold model for the effects of brood size (represented by curves 1–4) on the occurrence and timing of mate desertion. Larger broods have higher food demands and require higher food-delivery rates than smaller broods, resulting in a greater food supply needed to meet the monoparental threshold required for one parent to safely desert its mate without loss of offspring. Larger broods may also have a greater degree of asynchrony in hatching, which causes all nestlings to reach a peak probability of survival later than those from smaller broods. If parents desert after the young have reached a peak probability of survival, then smaller broods would reach a monoparental threshold, allowing one parent to safely desert its mate, earlier than larger broods. The effect of the brood-size manipulations on the occurrence and timing of desertion is shown by the arrows. Changing brood sizes should change the opportunity for one parent to desert by shifting the monoparental threshold.

monoparental threshold for desertion should be higher for larger broods, and the probability of desertion should vary accordingly (fig. 1). Second, mate desertion occurs significantly earlier for smaller broods than for larger ones and after nestlings have reached a peak probability of survival. Larger (more asynchronously hatched) broods may be deserted later because all nestlings reach a peak probability of survival later than those in smaller broods. Figure 1 shows the hypothetical relationship between the probability of all nestlings surviving (and, presumably, mate desertion) versus time after hatching for different brood sizes.

The model presented here relates parental-care patterns to reproductive benefits. It is similar to the marginal-value model of parental feeding effort of Patterson et al. (1980), which assumes that parental care can be given in small increments. However, marginal-value models are not particularly useful when investments must be made in large blocks (Patterson et al. 1980). Although some parental care can be given in increments (e.g., feeding nestlings), other types require all-or-none investments (e.g., incubating eggs). For the latter types of parental care, the functions in figure 1 occur as step functions, requiring some threshold value of investment to successfully raise all nestlings in broods of a given size. Mate desertion operates in this manner, since deserters completely terminate parental investments, whereas, at undeserted nests, mates assume nearly equal shares of parenting efforts (Beissinger 1987*b*; Beissinger and Snyder 1987).

The model (fig. 1) suggests that food supply and demand, brood size, and offspring age interact to create a monoparental threshold, at which two parents are no longer required to successfully raise the young. It assumes that parents can assess offspring age and local food supply in relation to demand by the brood. Parents can easily determine offspring age from the size and state of development of their young. Food supply, although more variable and unpredictable, may be assessed by rates of foraging success. The model also assumes that decreased parental investment is adaptive for deserters (Beissinger 1986), leading to fitness benefits either from reneating and increasing offspring production during the current breeding season (Trivers 1972; Maynard Smith 1977; Grafen and Sibley 1978) or from decreasing reproductive effort in the present bout, leading to increased survival or future fecundity (Reid 1987; Gustafsson and Sutherland 1988; Nur 1988). The model can be tested by experimentally manipulating food availability (supply) or brood sizes (demand) and determining if parents adjust their reproductive efforts by deserting their mates when a monoparental threshold is crossed.

In this paper, I examine the effect of brood size on the decision by kite parents to continue or to terminate parental care by deserting their mates. By changing brood sizes in experimental nests, I expected to shift the timing and perhaps the occurrence of mate desertion (fig. 1). Patterns of desertion at experimental nests are compared with those at unmanipulated nests from this study in Venezuela and from earlier work in Florida (Beissinger and Snyder 1987).

METHODS

This study was conducted from 1985 to 1987 in the llanos of Venezuela, low, flat plains that flood from May to December during the rainy season (Troth 1979; Sarmiento 1984) and dry completely during the dry season (January–April). Snail kites nest during the wet season (Mader 1981), and most appear to leave the llanos when they dry. I located kite nests by searching for adults exhibiting breeding behaviors (Beissinger 1988) on the ranch Fundo Pecario Masaguaral (state of Guarico; Eisenberg 1979) and along the main highway 30 km north and south of the ranch. Unlike the situation in Florida, where this species is endangered, snail kites are one of the most common raptors of the llanos, and a large tree can support a colony of up to 18 nests. In total, I found 264 kite nests, observing the fate of all but 13 through regular checks, usually one or two a week.

I determined the pattern of parental care at 28 unmanipulated nests and 28 experimental nests. Nests were designated as deserted when one parent was not observed feeding the young during a minimum of 15 h of observations spread over at least five different days (Beissinger and Snyder 1987). During nest watches, I observed parental-care behaviors for 1–5-h (usually 3-h) periods from blinds located 50–75 m away from nests, for a total of approximately 1,840 nest-hours of observations. I also recorded the number and type of food items brought to the nest by each parent.

Although no parents were banded, all young were individually color-banded. This permitted me to watch known family units in their nests and surrounding

marshes for 8–9 wk after hatching, 3–4 wk after the young began to fly but just 1–2 wk before they became completely independent from their parents (Beissinger and Snyder 1987). (This would not be possible for many passerines, which are both less visible and less likely to center their movements in one place after fledging.) Even though I could not determine the behavior of adults after they abandoned their mates and nests, it was clear when one parent had deserted because of its repeated absences (the sexes have obvious plumage differences; Beissinger 1988). The disappearance of a kite parent is, in most cases, likely to be due to desertion and not mortality because the regular disappearance of a parent (1) did not occur randomly throughout the nesting cycle, as might be expected if death were the cause, but only in the late nestling phase; (2) occurred in Florida only during years of good food production when the population grew exponentially, not during years of drought when food was scarce and the population crashed; (3) occurred in Venezuela only in broods of one or two young, and not in broods of three young as would be expected if mortality were due to stress or starvation; and (4) was followed once in Florida with telemetry, and the deserting female did not die but renested with a new mate immediately after deserting (Beissinger and Snyder 1987).

Brood size was manipulated at 20 nests in 1986 by adding or subtracting one or two young about 2 wk of age to create broods ranging in size from one to four young. (Clutch and brood sizes in Venezuela ranged from one to three, and hatching intervals, from 1 to 7 d.) Transferred chicks were similar in age and mass (which were usually intermediate) to the original chicks in experimental nests. On the basis of nest watches, all transferred young were accepted and fed by both of their new parents, and 86% ($n = 14$) of them fledged successfully. Results from these 20 experimental nests manipulated in 1986 are reported as one experiment. To increase sample size of enlarged broods, I created three more broods of four young each in 1987. Results for these four nests are presented separately. Nestlings also were exchanged at five other nests as part of an age-manipulation experiment not reported here except for data on which sex deserted. To increase nesting success, which is very low in this species (Beissinger 1986; Snyder et al. 1989), 21 of the 56 nests observed for desertion were protected from terrestrial predators using greased aluminum flashing around tree boles (Austad and Rabenold 1985).

Before experimentation at each nest, I verified through observations from blinds that both parents were actively feeding the brood, and I briefly visited the nest to weigh and measure young. Measurements of nestling wing length were used as an age estimator based on linear equations ($\text{age in days} = 0.097 \times \text{wing length} + 4.069$; $r^2 = 0.972$, $\text{SE} = 1.024$, $P < .001$) developed for Florida birds with wings longer than 40 mm (Beissinger 1984) after an analysis of covariance found no significant difference in the slopes ($P = .13$) or intercepts ($P = .49$) of wing growth for known-aged Florida and Venezuela nestlings. All young were color-banded at the time of experimentation. Thereafter, to minimize disturbance, nest sites were rarely, if ever, visited again. Watches from blinds were conducted every 3–4 d to determine if and when mate desertion occurred. Since the exact timing of mate desertion was seldom known, I used the midpoint between the last

date when both parents were observed and the first date when only one parent was present to estimate the date of desertion (average interval, 3.6 d; maximum, 5 d).

Nests were assigned experimental brood sizes based only on the number of young present and their ages in relation to other nearby nests available for manipulation. This method randomized for the effects of adult age, which I could not determine but does not affect reproductive output in Florida (Snyder et al. 1989), and parenting ability, which I could not control. However, two other factors that affect the costs and benefits of mate desertion could not be controlled and may have varied among nesting colonies (12 colonies total: 4 with both experimental and unmanipulated nests, 2 with only experimental nests, and 6 with only unmanipulated nests): (1) the operational sex ratio (Emlen and Oring 1977; Keenleyside 1983, 1985; but see Rogers 1987), since males in subadult plumage are indistinguishable from adult females yet fully capable of breeding successfully (Snyder et al. 1989); and (2) the local abundance of food (Townshend and Wootton 1985a; Beissinger and Snyder 1987). The benefit of deserting can also be affected by the amount of time remaining in the nesting season to find a new mate and renest (Maynard Smith 1977; Grafen and Sibley 1978; Beissinger and Snyder 1987). By manipulating broods in only one region, and within one month's time, I probably mitigated the effects of calendar time and variability in local food density on the timing and occurrence of mate desertion.

Statistical analyses were conducted using SYSTAT and SAS microcomputer programs. Means are reported with standard deviations and sample sizes (n). Parametric models were used when assumptions of normality and equality of variances were met. When these assumptions were violated, nonparametric statistics were used. Multiple-contingency models with maximum-likelihood estimates (Sokal and Rohlf 1981) were constructed to examine the six factors affecting the occurrence of desertion or which sex deserted (termed "full model"). However, the full model for the occurrence of desertion violated the assumptions of the multiple-contingency analysis because the limited sample size (56 nests) resulted in too many empty cells. To avoid this problem, I first tested for the effects of year and treatment (experimental or unmanipulated) and then eliminated them from the model (termed "partial model") to test for the effects of the remaining four factors. All models examined (full or partial multiple-contingency models, or single-classification χ^2 analyses) resulted in significance ($P < .05$) for the same effects, suggesting that the results are robust.

RESULTS

Pattern of Mate Desertion

Mate desertion occurred at about two-thirds of the 56 snail kite nests monitored for this behavior (table 1). The frequency with which nests were deserted did not differ between Venezuela and Florida ($\chi^2 = 1.9$, $df = 1$, $P > .15$; Beissinger and Snyder 1987). A partial multiple-contingency model found no differences ($P > .25$) either in the frequency of desertion between years of study or between manipulated and unmanipulated nests. Maximum-likelihood estimates of the effects of four other factors on the occurrence of mate desertion found only brood size to be significant ($P = .003$). (The relationship between brood size and mate desertion is

TABLE 1

THE FREQUENCY (AND PERCENTAGE) OF SNAIL KITE NESTS IN VENEZUELA AT WHICH EITHER ONE MATE DESERTED (MALE OR FEMALE) OR BOTH PARENTS REMAINED TO CARE FOR THE YOUNG

COMPARISON	n	DESERTED NESTS		UNDESERTED NESTS
		Male	Female	
Year				
1985	10	2 (20.0)	6 (60.0)	2 (20.0)
1986	34	7 (20.6)	13 (38.2)	14 (41.2)
1987	12	3 (25.0)	5 (41.7)	4 (33.3)
Total	56	12 (21.4)	24 (42.9)	20 (35.7)
Treatment				
Unmanipulated	28	8 (28.6)	10 (35.7)	10 (35.7)
Manipulated*	28	4 (14.3)	14 (50.0)	10 (35.7)

* Includes 23 nests at which broods were manipulated in 1986 and 1987, and 5 nests in 1986 and 1987 that were part of an age-manipulation experiment not reported here.

treated in detail in the following subsection.) None of the other factors affected the occurrence of mate desertion significantly ($P > .38$): (1) mate desertion was just as likely at nests in colonies (64.7%, $n = 51$) as at isolated nests (60.0%, $n = 5$); (2) protective flashing around the nest to discourage predators did not affect the occurrence of mate desertion (66.7% of 21 protected nests deserted vs. 62.9% of 35 unprotected nests); and (3) nests initiated in the early part of the breeding season (before June 19) were as likely to be deserted (58.3%, $n = 36$) as those begun later (50.0%, $n = 20$). Neither were there any significant interactions between brood size and any other factor. Clutch size was not considered in the partial-contingency model because data were missing for over half the nests; however, there was no difference (Fisher's exact test, $P = .40$) in the frequency of desertion at nests with two-egg clutches (73.3%, $n = 15$) versus three-egg clutches (63.6%, $n = 11$).

Overall, females deserted their mates twice as often as males ($\chi^2 = 4.0$, $df = 1$, $P < .05$), a pattern similar to Florida populations (Beissinger and Snyder 1987). Based on maximum-likelihood estimates from a full model, the sex that deserted was unaffected ($P > .50$) by year of study, brood size, protection from predators, degree of coloniality, or time of year; only treatment (experimental or unmanipulated) may have affected which mate deserted ($\chi^2 = 3.1$, $df = 1$, $P < .08$). Manipulated nests were deserted mostly by females, whereas unmanipulated nests were deserted by males nearly as often as by females (table 1). I can offer no explanation for female-biased desertions at experimental nests; like males, females accepted transplanted nestlings and fed them until desertion. Furthermore, nests where brood size was experimentally increased did not differ in the frequency of desertion by females from nests with experimentally decreased broods (five of six females deserted in both cases).

Brood Size, Fledging Success, and Mate Desertion

Fledging success was sharply reduced for broods that I enlarged (fig. 2). In the experiment, all broods of one or two young successfully fledged all young, and 80% of the young fledged from broods of three; but in broods of four, half the

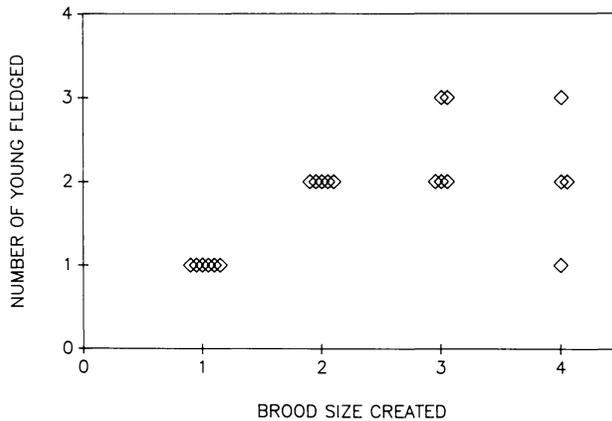


FIG. 2.—The number of young fledged from 20 snail kite nests when brood size was manipulated by adding or subtracting one or two young in 1986.

young died. No parents raised four young, and only 40% of the nests receiving three young fledged them all. Just three of the nine pairs that at one time had three or more chicks were able to fledge three young (fig. 2). When three more broods were enlarged to four young in 1987, I found similar results (fledging of one, two, and three young). Thus, at experimental nests, two kite parents were unable to raise four young ($n = 7$ nests total) in Venezuela and often had trouble raising three young successfully.

Fledging success at unmanipulated nests was similar to success at experimental nests. No broods of three young occurred naturally in Venezuela ($n = 205$ nests where the fate was known). Of 51 unmanipulated nests in this study known to have fledged young, none fledged three young, even though 37% would have contained three-egg clutches if the frequency of their occurrence in Venezuela held here (Beissinger, unpublished manuscript). In Florida, however, broods of three young are fledged as often as broods of one, about 22% of the time (Beissinger 1986; Snyder et al. 1989), and frequently are deserted by one parent (Beissinger and Snyder 1987).

There was little direct evidence of the causes of offspring death in most of the experimentally enlarged nests, a common problem in other studies of this species (Snyder et al. 1989). Although their nest mates were unharmed, doomed young usually disappeared one at a time as nestlings from experimental broods of three and four young ($n = 8$ broods), except twice when fledglings died shortly after leaving the nest. Observations of kite chicks revealed no aggressive behaviors that commonly precede siblicide (see, e.g., Newton 1979; Mock 1984, 1985). The pattern of offspring mortality at most experimental nests was probably not the result of predation, since predators usually destroy the whole nest (Ricklefs 1969; Pettingill 1976) and did so in the four instances of avian predation that we witnessed directly (for complete brood loss to snakes and mammals, see Bennetts and Caton 1988; Snyder et al. 1989). Instead, the slow, partial attrition of most experimentally enlarged broods suggests that offspring mortality may have been primarily due to starvation.

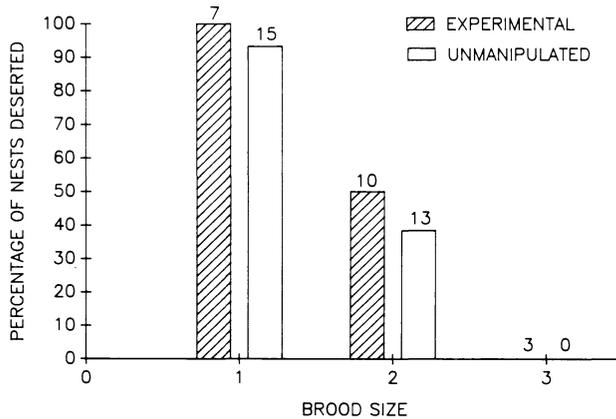


FIG. 3.—The percentage of nests deserted by one snail kite parent in relation to brood size. Experimental nests had brood size manipulated by adding or subtracting one or two young in 1986. Sample sizes are shown above each bar.

That offspring mortality in enlarged broods could have been due to starvation is supported by analyses of food-delivery rates to the nestlings and diet composition. Although delivery rates of food by two parents increased significantly with brood size ($F = 24.8$, $df = 3, 265$, $P < .001$), means for brood sizes differed significantly only between broods of one young and the others, not between broods of two or more young (Tukey's honestly significant difference, $P < .05$): deliveries per hour were 1.70 ± 0.87 SD, 2.49 ± 1.08 , 3.16 ± 0.80 , and 3.11 ± 1.10 during observation periods for broods of one ($n = 109$), two ($n = 122$), three ($n = 29$), and four ($n = 9$), respectively. Delivery rates in Venezuela were significantly lower (1–1.5 deliveries per hour) than rates for same-sized broods in Florida, except for broods of one young, which were equivalent (Beissinger and Snyder 1987; Beissinger, unpublished manuscript). Moreover, kite parents in Venezuela fed lower-quality food to nestlings (Beissinger 1990): freshwater crabs (*Dilocarcinus dentatus*), which require much longer handling times and are usually less profitable than snails, accounted for more than 10% of the food items, exceeding 25% in some months.

Brood size was the most important factor determining the occurrence of mate desertion (fig. 3). Desertion occurred at all of the 1986 experimental nests fledging one young, at half of the nests fledging two young, and at none of the three nests that fledged three young. Similar patterns occurred for the unmanipulated nests (fig. 3). Examination of all 56 nests (table 1; fig. 3) shows that all but one of the 28 broods of one young were deserted during this study, a little less than half (41.7%) of the 24 broods of two young were deserted, and none of the four broods of three young were deserted. Maximum-likelihood analyses showed that the occurrence of mate desertion was significantly affected by brood size ($P < .003$) but not by experimental treatment ($P = .30$).

If most offspring mortality was presumably caused by starvation, then results from this experiment suggest that kite parents might respond to brood size, as it relates to food demand by the nestlings and food availability, in deciding whether

TABLE 2

FEEDING RATES AND DIET COMPOSITION FOR BROODS OF TWO YOUNG AT DESERTED NESTS BEFORE MATE DESERTION OCCURRED AND AT NESTS NOT DESERTED BY ONE PARENT

Comparison	Deserted	Undeserted	<i>P</i> *
Feeding rate (trips per hour)			
Experimental nests	2.24 ± .48 (4)	2.61 ± .65 (5)	.44
All nests	2.29 ± .55 (7)	2.47 ± .81 (14)	.62
Percentage of snails in diet			
Experimental nests	79 ± 28 (4)	87 ± 9 (5)	.56†
All nests	84 ± 23 (7)	89 ± 14 (14)	.92†

NOTE.—Values are means per nest, based on multiple observations, ± one standard deviation (the number of nests is in parentheses).

* Probability values for Student's *t*-test.

† Percentages were arcsine-transformed before testing to approximate normality.

TABLE 3

THE TIMING OF MATE DESERTION BY A SNAIL KITE PARENT IN RELATION TO BROOD SIZE AND THE OCCURRENCE OF BROOD REDUCTION BEFORE DESERTION

BROOD REDUCTION	BROOD SIZE FLEDGED	
	1	2
No	24.0 ± 5.0 (10)	32.8 ± 12.8 (5)
Yes	39.7 ± 6.7 (9)	30.0 ± 2.8 (2)

NOTE.—Values are mean days to desertion after hatching of the oldest chick in the nest ± one standard deviation (the number of nests is in parentheses).

to desert their mates or not. One test of the importance of food in determining whether mate desertion will occur is to compare food-delivery rates between deserted and undeserted nests; both types of nests occurred only among broods of two young. There were no significant differences in the number of food items delivered per hour between deserted and undeserted nests either for experimental nests or for all nests with two young (table 2). Neither did snails compose a significantly greater proportion of the diet at deserted than at undeserted nests (table 2).

Timing of Mate Desertion

Brood size was expected to correlate positively with the timing of mate desertion (fig. 1). Over all nests, however, broods of one young were not deserted earlier (31.9 d ± 9.8 SD, *n* = 19) than broods of two young (32.0 d ± 10.6, *n* = 7). This result was primarily an effect of brood reduction on the timing of mate desertion (table 3). A two-way analysis of variance (*n* = 27, *r*² = 0.39) found that brood size was an important factor affecting the timing of desertion (*F* = 3.41, *df* = 1, *P* = .078) and brood reduction was not (*F* = 0.69, *df* = 1, *P* = .414), but a significant interaction occurred (*F* = 7.6, *df* = 1, *P* = .011).

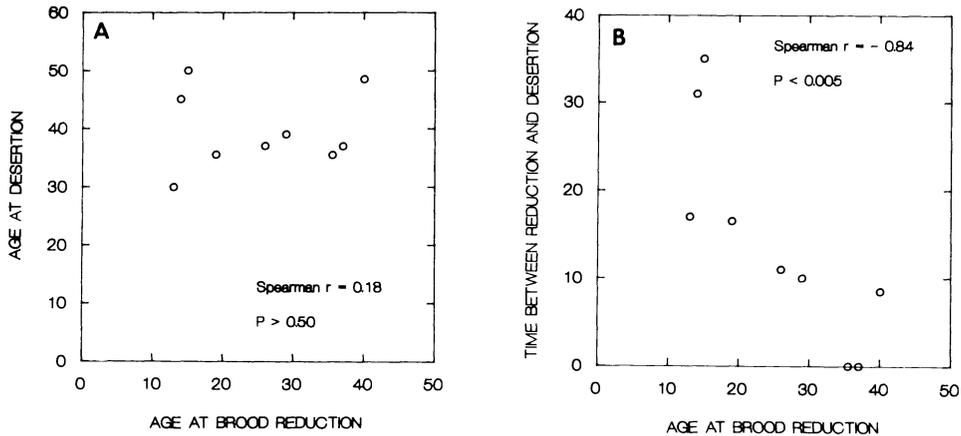
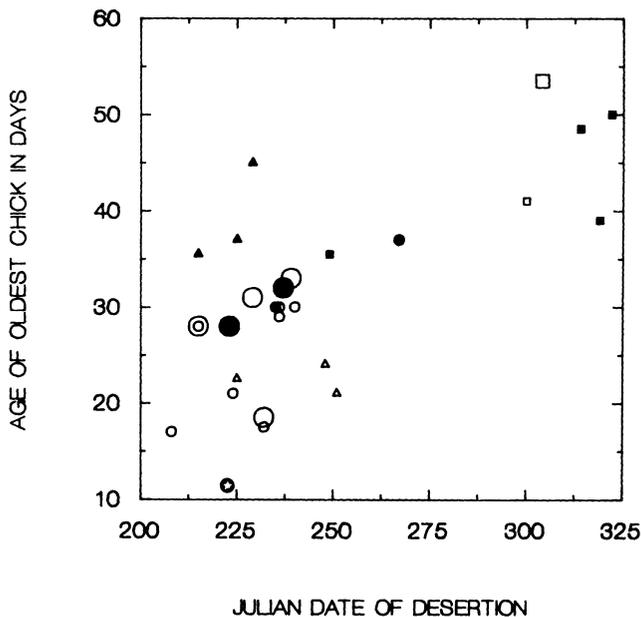


FIG. 4.—The relationship between the age at which two-young broods were reduced to one young and A, the age in days of the remaining nestling when mate desertion occurred, or B, the amount of time after brood reduction until one parent deserted.

The interaction between brood size and brood reduction on the timing of mate desertion was an effect of the timing of desertion of one-young broods (table 3). Mate desertion frequently followed within a week of brood reduction, which occurred up to 3–6 wk after hatching. If a brood was reduced from two to one young in the latter part of the nestling stage (e.g., 3–5 wk of age), desertion nearly always occurred (fig. 3) but was delayed simply because neither parent had deserted previously. A better test of the effects of brood size on the timing of desertion would be to compare timing among the 10 experimental broods of one or two young where brood reduction did not occur (fig. 2). Among these nests, there was a tendency (one-tailed test, $U = 8$, $P < .10$) for one parent of broods of one young to desert earlier ($\bar{x} = 24.7 \text{ d} \pm 6.4$, $n = 5$) than one parent of broods of two ($\bar{x} = 28.8 \text{ d} \pm 5.1$, $n = 5$). Similar results were observed at unmanipulated nests in Florida (Beissinger and Snyder 1987).

That kites frequently delayed desertion of broods of two young until one of the young died suggests that parents flexibly adjusted the timing of desertion after brood reduction. Only once in Venezuela ($n = 26$ nests with complete data) did brood reduction occur after mate desertion, although, in four other cases, the exact timing of mate desertion and brood reduction could not be determined. Although no significant relationship existed between the timing of brood reduction at unmanipulated nests with two young and the age of the young when one mate deserted (fig. 4A), mate desertion did occur significantly sooner after brood reduction when reduction occurred at an advanced age (fig. 4B).

If one of the most important benefits of deserting is to find a new mate and renest (Beissinger and Snyder 1987), mate desertion might be expected to occur more rapidly during the earlier, rather than the later, part of the breeding season. This prediction was supported by a strong positive relationship (fig. 5) between Julian date of desertion and the timing of mate desertion (Pearson $r = 0.702$, $n =$



with three-egg clutches ($27.5 \text{ d} \pm 13.5$, $n = 6$). Although males tended to desert their mates earlier ($27.8 \text{ d} \pm 10.6$, $n = 8$) than did females ($32.5 \text{ d} \pm 10.3$, $n = 20$), the difference was not significant ($t = 1.1$, $df = 26$, $P = .28$), and the sex of the deserter was not a significant covariate ($F = 0.08$, $P = .78$) with Julian date of desertion.

DISCUSSION

Brood Size, Food Supply, and Parental-Care Patterns

Previous research has stressed how ecological factors, such as the distribution and defensibility of resources and mates, have influenced the evolution of mating systems (Lack 1968; Orians 1969; Emlen and Oring 1977; Wittenberger 1979; Oring 1982). Only more recently has attention been paid to the importance of clutch or brood size as a factor affecting mating systems through parental-care patterns (Walters 1982; Beissinger 1986; Whittingham 1989).

This study demonstrates how brood size can act as a proximate factor controlling the mating system through the demands of parental care. Observational studies of birds with variable mating systems have shown that brood size can influence which sex deserts (Beissinger and Snyder 1987; Persson and Öhrstrom 1989) and whether desertion occurs (Fujioka 1989). Prior to this study, the only experimental tests of the influence of brood size on the allocation of reproductive effort between broods were conducted on polygynous male blackbirds (*Agelaius phoeniceus* and *Xanthocephalus xanthocephalus*) and yielded conflicting results (Patterson et al. 1980; Muldal et al. 1986; Whittingham 1989). In this study of snail kite nests with both manipulated and unmanipulated brood sizes (fig. 3), the effect of brood size on the allocation of reproductive effort was clear: mate desertion nearly always occurred when broods were small (one young), occurred in medium-sized broods (two young) slightly less than half the time, and did not occur in large broods (three young).

That both kite parents remained to care for large broods, whereas one adult nearly always deserted small broods, suggests that snail kite parents flexibly adjust their parental investments according to the expected benefits of reproduction (Trivers 1972; Robertson and Bierman 1979; Patterson et al. 1980) and the need for biparental care (Gowaty 1983; Wolf et al. 1988). A similar adjustment, in the form of nest abandonment, may occur in egrets, herons, and ducks (Mock and Parker 1986; Armstrong and Robertson 1988).

Both food supply and brood size have been shown to be important determinants of the patterns of parental care exhibited by vertebrates. For example, food supply has been implicated as a determinant of parental investment in fish (Townshend and Wootton 1985b) and birds (Lott 1984; Beissinger and Snyder 1987; Martin 1987). Brood size can affect the amount and type of parental care invested (Andersson et al. 1980; Carlisle 1982, 1985; Hegner and Wingfield 1987; Lessells 1987; Schindler and Lamprecht 1987).

In this study, food supply and food demand by nestlings probably interacted to create a monoparental threshold (fig. 1), affecting the opportunity for one parent to desert its mate. The interaction between brood size, food supply, and parental-

care patterns is suggested from several results: (1) mate desertion occurred at nests with small, but not large, brood sizes, (2) two parents attending experimental nests were unable to raise four young and had difficulty raising broods of three, (3) although broods of three are commonly fledged in Florida (Beissinger 1986; Snyder et al. 1989), no natural broods of three fledged in Venezuela, (4) evidence from experimentally enlarged broods suggested that offspring mortality was due to starvation rather than predation or siblicide, and (5) food-delivery rates did not increase proportionally to support experimentally enlarged broods and were substantially lower, except for broods of one young, at Venezuelan nests than at Florida nests.

These results, taken together, indicate that food supply may function as an ultimate factor in determining the occurrence of mate desertion in Venezuelan kites by limiting brood size. Brood size and food supply would then interact to determine the necessity for biparental care throughout the complete nesting cycle (rarely for small broods, usually for large broods, sometimes for medium broods), allowing kite parents to flexibly adjust their parental efforts through mate desertion. Adjusting parental effort through mate desertion is an alternative strategy that, instead of monogamy, could be found in other bird species with biparental care if (1) breeding seasons are long relative to the nest cycle, (2) the need for biparental care decreases during the nest cycle, and (3) the costs associated with establishing a new territory or nest site are minimal (Beissinger 1986; Fujioka 1989).

Food supply could also act as a proximate determinant of mate desertion if kite parents adjust their parental efforts in relation to local variation in food supplies. Such an adjustment should have occurred in kite broods of two young. Although food supply was not manipulated, observations of food delivered to deserted and undeserted broods of two found no significant difference in feeding rates or the percentage of crabs (low-quality food) in the diet. Several problems arise when using food-delivery rates as estimates of food availability. Variation in delivery rates might occur if potential deserters "tested" their mate's ability to care for the young by decreasing food deliveries before desertion (Beissinger 1987*b*), and this could partly account for the lack of difference in delivery rates between deserted and undeserted nests. Although a higher food-delivery rate can be associated with greater levels of local food availability (Beissinger and Snyder 1987), it may also be an effect of individual differences among parents in hunting ability or experience. Alternatively, local variation in food supply may have interacted with other factors I was not able to measure or control in this study, such as the operational sex ratio or age of parents, which also play an important role in desertion decisions (Emlen and Oring 1977; Maynard Smith 1977).

Female snail kites deserted their mates more often than males did, both in Venezuela and in Florida. This pattern occurred in every year in Venezuela (table 1) but not in Florida (Beissinger and Snyder 1987). Why females are more likely to desert their mates is unclear. Because the operational sex ratio is difficult to measure in snail kites, it is not known if a consistent skew toward males exists; such a skew could be responsible for the bias toward female desertions. In Florida, however, females deserted primarily small and medium-sized broods,

whereas males deserted mostly large ones (Beissinger and Snyder 1987). Parental investment influenced which parent deserted, primarily through the role that each parent assumed in feeding the young; deserters participated less in this activity (Beissinger 1987*b*). Because a male snail kite invests more reproductive effort before egg laying than does the female (Beissinger 1987*a*) and assumes equal portions of incubation duties (Beissinger 1987*b*), it has been suggested that female reproductive effort is unlikely to exceed male effort until late in the brood-rearing stage (Beissinger and Snyder 1987). This would be more likely to occur with large broods, since they require more food and more time for all nestlings to reach a peak probability of survival. Unfortunately, this hypothesis could not be tested in Venezuela because large broods were not deserted by either parent.

Factors Affecting the Timing of Desertion

Brood size also affected the timing of mate desertion by snail kites but less strongly than it affected the occurrence of desertion. In part, this was because brood size and the occurrence of brood reduction interacted to affect the timing of mate desertion (table 2). When small broods were the result of larger broods that experienced brood reduction in the later nestling stages, mate desertion usually followed shortly thereafter, but the timing was frequently retarded compared with nests that did not experience brood reduction. The effects of brood size on the timing of mate desertion could more clearly be seen in experimental broods that were not reduced: small broods tended to be deserted sooner than medium-sized broods. Parents also appeared to desert sooner if brood reduction occurred when the brood was older (fig. 4*B*). Perhaps parents time their desertion to coincide with some threshold of offspring age. The fact that brood reduction rarely occurs after mate desertion in Venezuela (3.8%) or in Florida (4%; Beissinger and Snyder 1987) suggests that this threshold coincides with the period when offspring survival is nearly ensured. The earliest this could occur would be after the young no longer need to be brooded (about 2 wk of age; Beissinger 1987*b*). The variability in the timing of desertion after this age (figs. 4*A*, 5), however, suggests that factors other than brood size and offspring age must affect the timing of mate desertion.

For instance, nests initiated early in the breeding season were generally deserted sooner than nests begun at a later date (fig. 5). Since deserters can renest immediately with a new mate (Beissinger and Snyder 1987), individuals that desert early in the breeding season have more time to renest, perhaps the most important benefit of mate desertion (Maynard Smith 1977; Grafen and Sibley 1978). However, nests begun late in the breeding season were also deserted, suggesting that a deserter may benefit from decreased reproductive effort (Beissinger and Snyder 1987). Differences between years in the timing of mate desertion were probably due to year-to-year variation in the onset of the rainy season, which influences the initiation of nesting, and the amount of rainfall, which, in conjunction with water levels, determines food availability.

Brood-Size-Manipulation Experiments and Clutch Size in Tropical Birds

Skutch (1949, 1985) argued that predation, not a limitation in food supply or harvesting potential (Lack 1947, 1968; Klomp 1970), was responsible for the

latitudinal decline in clutch size approaching the equator. To the best of my knowledge, nearly all experimental evidence for the importance of food as a factor limiting clutch size is derived from temperate-zone birds (reviews in Winkler and Walters 1983; Murphy and Haukioja 1986; Hegner and Wingfield 1987; Martin 1987). Besides this study, clutch or brood sizes of tropical land birds have been manipulated only by Ward (1965), Morton (1971, personal communication), Mader (1982), and Tarburton (1987). Although Ward's results were inconclusive, the clay-colored robin (*Turdus grayi*), savannah hawk (*Buteogallus meridionalis*), white-rumped swiftlet (*Aerodramus spodiopygius*), and snail kite were all unable to raise enlarged broods. Snail kite parents could not raise four young, had trouble raising three young, and did not increase feeding rates proportionally for these broods before brood reduction occurred. Enlarged kite broods (four chicks) fledged fewer young than small and medium-sized broods (fig. 2). Thus, results from the few experimental studies conducted on tropical land birds support Lack's contention that clutch and brood sizes may be limited by food.

Both clutch and brood sizes in snail kites declined with latitude, being nearly 0.3 eggs and 0.5 young per successful nest smaller in Venezuela than in Florida (Beissinger 1986, unpublished manuscript; Snyder et al. 1989). The absence of successful broods of three young in Venezuela, coupled with lower food-delivery rates to nestlings there compared with Florida, suggests that food may play a more important role in limiting reproductive output in Venezuelan kites than in the endangered Florida population. In support of this possibility, Venezuelan snail kites expanded their diet during the breeding season to include less-profitable crabs (Beissinger 1990).

CONCLUSIONS

Results from this and other studies (Walters 1982; Lazarus and Inglis 1986; Morris 1987; Winkler 1987; Whittingham 1989) suggest that variation in mating systems and parental-care patterns is not due simply to variation in the resource base per se but to the demand placed on that base by the expected benefit (clutch or brood size) and cost (parental investment) of reproduction. By manipulating the brood size of snail kite nests, I showed how brood size and, to a lesser extent, offspring age interact with the food supply and demand to create a monoparental threshold (fig. 1). This threshold, as reflected by both the occurrence (fig. 3) and the timing of mate desertion, is crossed if food supplies are sufficient to permit one parent to support a brood of young that has reached peak survival potential (Beissinger and Snyder 1987). By choosing to desert or not, a kite parent can adjust its parental investment in relation to the factors influencing the benefits of the present reproductive bout (i.e., the number of offspring and their age) as well as to those factors affecting the chance to nest again in the future.

SUMMARY

The effect of brood size (the expected benefit of reproduction) on the decision of a snail kite parent to desert its mate or not was examined by manipulating brood

size (normally one to three young). Mate desertion occurred at about two-thirds of the nests monitored, with females deserting twice as often as males. Fledging success was sharply reduced for enlarged broods: kite parents had difficulty raising three young and were unable to raise four young. Low food-delivery rates, coupled with partial brood reductions of enlarged broods, indicated that starvation was the most likely cause of most offspring mortality. Desertion occurred at all experimental nests fledging one young, at half of the nests fledging two young, and at none of the few nests that were able to fledge three young. Similar patterns of fledging success and desertion were found for unmanipulated nests, except that parents attending unmanipulated nests were unable to fledge three young successfully. The occurrence of mate desertion was not related to clutch size, Julian date of nest initiation, or whether nests were colonial or solitary. Deserted nests fledging two young did not have higher food-delivery rates than undeserted counterparts. Desertion tended to occur earlier in one-young broods than in two-young broods after the effects of brood reduction were considered. Nests begun earlier in the breeding season were deserted earlier than those begun later; differences also existed between years.

These results demonstrate how brood size can act as a proximate factor controlling the mating system through the demands of parental care. A monoparental threshold, as reflected by both the occurrence and the timing of desertion, is based on the relationship between food demand (by the brood) and supply, and it can be crossed if a single parent is capable of caring for the offspring alone. That snail kite parents of experimentally enlarged broods could not fledge four young, had difficulty fledging three young, and did not increase food-delivery rates proportionally with brood size supports Lack's hypothesis that food limits clutch size in tropical birds.

ACKNOWLEDGMENTS

Financial support for this work was provided by the National Zoological Park, a National Science Foundation Postdoctoral Fellowship in Environmental Biology, the Smithsonian Institution's International Environmental Sciences Program, the American Museum of Natural History, and the University of Florida. Tomas Blohm kindly allowed me to live and work on his ranch. Sincere thanks to the many Venezuelan landowners who graciously permitted me access to kite nests on their property. G. DiChiro, G. Hernandez, M. F. Rodriguez, K. Silvius, and R. Thorstrom assisted in fieldwork. M. Soulé helped me to prepare figure 1. I appreciate reviews of this paper by M. Fujioka, P. A. Gowaty, R. Greenberg, E. S. Morton, N. F. R. Snyder, C. Wiklund, S. Zack, and the anonymous New Haven "reviewer" who broke into my car to "read" this manuscript but "rejected" it in a locale where it was later found.

LITERATURE CITED

- Alexander, R. D., and G. Borgia. 1979. On the origin and basis of the male-female phenomenon. Pages 417-440 in M. S. Blum and N. A. Blum, eds. *Sexual selection and reproductive competition in insects*. Academic Press, New York.

- Andersson, M., C. G. Wiklund, and H. Rundgren. 1980. Parental defense of offspring: a model and an example. *Anim. Behav.* 28:536–542.
- Armstrong, T., and R. J. Robertson. 1988. Parental investment based on clutch value: nest desertion in response to partial clutch loss in dabbling ducks. *Anim. Behav.* 36:941–943.
- Austad, S. N., and K. N. Rabenold. 1985. Reproductive enhancement and an experimental inquiry into its mechanism in the bicolored wren. *Behav. Ecol. Sociobiol.* 17:19–27.
- Beissinger, S. R. 1984. Mate desertion and reproductive effort in the snail kite. Ph.D. diss. University of Michigan, Ann Arbor.
- . 1986. Demography, environmental uncertainty, and the evolution of mate desertion in the snail kite. *Ecology* 67:1445–1459.
- . 1987a. Anisogamy overcome: female strategies in snail kites. *Am. Nat.* 129:484–500.
- . 1987b. Mate desertion and reproductive effort in the snail kite. *Anim. Behav.* 35:1504–1519.
- . 1988. The snail kite. Pages 148–165 in R. S. Palmer, ed. *Handbook of North American birds*. Vol. IV. Yale University Press, New Haven, Conn.
- . 1990. Alternative foods of a diet specialist, the snail kite. *Auk* 107:327–333.
- Beissinger, S. R., and N. F. R. Snyder. 1987. Mate desertion in the snail kite. *Anim. Behav.* 35:477–487.
- Bennetts, R. E., and E. L. Caton. 1988. An observed incident of rat predation on snail kite (*Rosthamus sociabilis*) chicks in Florida. *Fla. Field Nat.* 16:14–16.
- Boucher, D. H. 1977. On wasting parental investment. *Am. Nat.* 111:786–788.
- Carlisle, T. R. 1982. Brood success in variable environments: implications for parental care allocation. *Anim. Behav.* 30:824–836.
- . 1985. Parental response to brood size in a cichlid fish. *Anim. Behav.* 33:234–238.
- Davies, N. B., and A. Lundberg. 1984. Food distribution and a variable mating system in the dunnock, *Prunella modularis*. *J. Anim. Ecol.* 53:895–912.
- Dawkins, R., and T. R. Carlisle. 1976. Parental investment, mate desertion and a fallacy. *Nature (Lond.)* 262:131–132.
- Drent, R. H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–252.
- Eisenberg, J. F., ed. 1979. *Vertebrate ecology in the northern Neotropics*. Smithsonian Institution Press, Washington, D.C.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science (Washington, D.C.)* 197:215–233.
- Fujioka, M. 1989. Mate and nestling desertion in colonial little egrets. *Auk* 106:292–302.
- Gowaty, P. A. 1983. Male parental care and apparent monogamy in eastern bluebirds (*Sialia sialis*). *Am. Nat.* 112:149–157.
- Grafen, A., and R. Sibley. 1978. A model of mate desertion. *Anim. Behav.* 26:645–652.
- Gustafsson, L., and W. J. Sutherland. 1988. The costs of reproduction in the collared flycatcher *Ficedula albicollis*. *Nature (Lond.)* 335:813–815.
- Haverschmidt, F. M. 1962. Notes on the feeding habits and food of some hawks of Surinam. *Condor* 64:154–158.
- Hegner, R. E., and J. C. Wingfield. 1987. Effects of brood-size manipulations on parental investment, breeding success, and reproductive endocrinology of house sparrows. *Auk* 104:470–480.
- Keenleyside, M. H. A. 1983. Mate desertion in relation to adult sex ratio in the biparental cichlid fish *Herotilapia multispinosa*. *Anim. Behav.* 31:683–688.
- . 1985. Bigamy and mate choice in the biparental *Cichlasoma nigrofasciatum*. *Behav. Ecol. Sociobiol.* 17:285–290.
- Klomp, H. 1970. The determination of clutch-size in birds—a review. *Ardea* 58:1–124.
- Lack, D. 1947. The significance of clutch size. *Ibis* 89:302–352.
- . 1968. *Ecological adaptations for breeding in birds*. Methuen, London.
- Lazarus, J., and I. R. Inglis. 1986. Shared and unshared parental investment, parent-offspring conflict and brood size. *Anim. Behav.* 34:1791–1804.
- Lessells, C. M. 1987. Parental investment, brood size and time budgets: behaviour of lesser snow goose families. *Ardea* 75:189–203.

- Lott, D. F. 1984. Intraspecific variation in the social systems of wild vertebrates. *Behaviour* 88: 266–325.
- Mader, W. J. 1981. Notes on nesting raptors in the llanos of Venezuela. *Condor* 83:48–51.
- . 1982. Ecology and breeding habits of the savanna hawk in the llanos of Venezuela. *Condor* 84:261–271.
- Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annu. Rev. Ecol. Syst.* 18:453–487.
- Maynard Smith, J. 1977. Parental investment: a prospective analysis. *Anim. Behav.* 25:1–9.
- Mock, D. W. 1984. Infanticide, siblicide, and avian mortality. Pages 3–30 *in* G. Hausfater and S. B. Hrdy, eds. *Infanticide: evolutionary and comparative perspectives*. Aldine, New York.
- . 1985. Siblicidal brood reduction: the prey-size hypothesis. *Am. Nat.* 125:327–343.
- Mock, D. W., and G. A. Parker. 1986. Advantages and disadvantages of egret and heron brood reduction. *Evolution* 40:459–470.
- Morris, D. W. 1987. Optimal allocation of parental investment. *Oikos* 49:332–339.
- Morton, E. S. 1971. Nest predation affecting the breeding season of the clay-colored robin, a tropical song bird. *Science (Washington, D.C.)* 171:920–921.
- Muldal, A., J. D. Moffatt, and R. J. Robertson. 1986. Parental care of nestlings by male red-winged blackbirds. *Behav. Ecol. Sociobiol.* 19:105–114.
- Murphy, E. C., and E. Haukioja. 1986. Clutch size in nidicolous birds. *Curr. Ornithol.* 4:141–210.
- Newton, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, S. Dak.
- Nur, N. 1988. The consequences of brood size for breeding tits. III. Measuring the costs of reproduction: survival, future fecundity, and differential dispersal. *Evolution* 42:351–362.
- Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. *Am. Nat.* 103:589–603.
- Oring, L. W. 1982. Avian mating systems. *Avian Biol.* 6:1–92.
- Patterson, C. B., W. J. Erckmann, and G. H. Orians. 1980. An experimental study of parental investment and polygyny in male blackbirds. *Am. Nat.* 116:757–769.
- Persson, O., and P. Öhrstrom. 1989. A new avian mating system: ambisexual polygamy in the penduline tit *Remiz pendulinus*. *Ornis Scand.* 20:105–111.
- Pettingill, O. S., Jr. 1976. Observed acts of predation on birds in northern lower Michigan. *Living Bird* 15:33–41.
- Reid, W. V. 1987. The cost of reproduction in the glaucous-winged gull. *Oecologia (Berl.)* 74:458–467.
- Ricklefs, R. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* 9:1–48.
- Robertson, R. J., and G. C. Biermann. 1979. Parental investment strategies determined by expected benefits. *Z. Tierpsychol.* 50:124–128.
- Rogers, W. 1987. Sex ratio, monogamy and breeding success in the Midas cichlid. *Behav. Ecol. Sociobiol.* 21:47–51.
- Sarmiento, G. 1984. *The ecology of Neotropical savannas*. Harvard University Press, Cambridge, Mass.
- Schindler, M., and J. Lamprecht. 1987. Increase of parental effort with brood size in a nidifugous bird. *Auk* 104:688–693.
- Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91:430–455.
- . 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. *Ornithol. Monogr.* 36:575–594.
- Snyder, N. F. R., S. R. Beissinger, and R. E. Chandler. 1989. Reproduction and demography of the Florida everglade (snail) kite. *Condor* 91:300–316.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. 2d ed. W. H. Freeman, New York.
- Stearns, S. C. 1976. Life-history tactics: a review of ideas. *Q. Rev. Biol.* 51:3–47.
- Tarburton, M. K. 1987. An experimental manipulation of clutch and brood size of white-rumped swiftlets *Aerodramus spodiopygius* of Fiji. *Ibis* 129:107–114.
- Thompson, S. D., and M. E. Nicoll. 1986. Basal metabolic rate and energetics of reproduction in therian mammals. *Nature (Lond.)* 321:690–693.
- Townshend, T. J., and R. J. Wootton. 1985a. Variation in the mating system of a biparental cichlid fish, *Cichlasoma panamense*. *Behaviour* 95:181–197.
- . 1985b. Adjusting parental investment to changing environmental conditions: the effect of food

- ration on parental behaviour of the convict cichlid, *Cichlasoma nigrofasciatum*. *Anim. Behav.* 33:494–501.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136–179 in B. Campbell, ed. *Sexual selection and the descent of man, 1871–1971*. Aldine, Chicago.
- Troth, R. G. 1979. Vegetational types on a ranch in the central llanos of Venezuela. Pages 17–30 in J. F. Eisenberg, ed. *Vertebrate ecology in the northern Neotropics*. Smithsonian Institution Press, Washington, D.C.
- Walsberg, G. E. 1983. Avian ecological energetics. *Avian Biol.* 7:161–220.
- Walters, J. R. 1982. Parental behavior in lapwings (Charadriidae) and its relationships with clutch sizes and mating systems. *Evolution* 36:1030–1040.
- Ward, P. 1965. The breeding biology of the black-faced dioch, *Quelea quelea*, in Nigeria. *Ibis* 107:326–349.
- Whittingham, L. A. 1989. An experimental study of paternal behavior in red-winged blackbirds. *Behav. Ecol. Sociobiol.* 25:73–80.
- Winkler, D. W. 1987. A general model for parental care. *Am. Nat.* 130:526–543.
- Winkler, D. W., and J. R. Walters. 1983. The determination of clutch size in precocial birds. *Curr. Ornithol.* 1:33–68.
- Wittenberger, J. F. 1979. The evolution of mating systems in birds and mammals. Pages 271–349 in P. Marler and J. G. Vandenbergh, eds. *Handbook of behavioral neurobiology*. Vol. 3. Plenum, New York.
- Wolf, L., E. D. Ketterson, and V. Nolan, Jr. 1988. Paternal influence on growth and survival of dark-eyed junco young: do males benefit? *Anim. Behav.* 36:1601–1618.