Beissinger, S. '87

Anim. Behav., 1987, **35**, 477–487

Mate desertion in the snail kite

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Abstract. Mate desertion during the breeding cycle was documented at 28 of 36 (78%) snail kite, *Rostrhamus sociabilis* nests in Florida between 1979 and 1983. Offspring mortality occurred at only one deserted nest, however. Parents that were deserted by their mates continued to care for their young until independence (3–5 additional weeks) and provided snails at a rate similar to that of both parents combined before desertion. Males and females deserted with nearly equal frequency, except in 1982 when more females deserted. No desertion occurred during drought years, whereas desertion occurred at nearly every nest during favourable conditions. The occurrence of mate desertion was generally related to indirect measures of snail abundance: foraging range, snail delivery rates to the young and growth rates. Small broods were deserted more frequently by females than by males and tended to be deserted earlier than large ones. After desertion, deserters had the opportunity to re-mate and nest again since breeding seasons were commonly lengthy, but whether they did so was impossible to determine conclusively in most cases. The deserted bird sometimes incurred increased energetic costs and lost breeding opportunities during periods of monoparental care.

In many animals, parents may abort a reproductive attempt by deserting their offspring when environmental conditions jeopardize adult survival (e.g. Schreiber & Ashmole 1970; Kynard 1978; Nelson 1978; Tait 1980). Desertion may also occur when conditions permit one parent to care for the offspring as effectively as two. Under such circumstances, mate deserters may be able to increase their fitness by re-mating or escaping parental duties, which are assumed by the remaining mate. Desertion of this second kind can lead to polygyny or polyandry and is common among fishes (Blumer 1979; Perrone & Zaret 1979), reptiles and amphibians (Ridley 1978; Wells 1981) and mammals (Kleiman 1977), but is relatively rare in birds (Lack 1968; Oring 1982).

In almost all species where it occurs, mate desertion is characteristic of only one sex (Emlen & Oring 1977; Kleiman 1977; Ridley 1978; Wittenberger 1981; Oring 1982). Mate desertion by either sex, ambisexual mate desertion, occurs rarely in birds. It has been recorded very infrequently in the house wren (*Troglodytes aedon*, Kendeigh 1941) and also in Tengmalm's owl (*Aegolius funereus*, Solheim 1983), although the frequency of mate desertion in this species is unknown. The dunnock, *Prunella modularis*, is both polygynous and polyandrous (Davies & Lundberg 1984). However, this mating system results from the influence of the spatial arrangement of food resources on the settling patterns of adults through the ability of males to control access to females, not from mate desertion per se.

In this report, however, we describe a regular pattern of mate desertion for the endangered Florida snail (Everglade) kite, *Rostrhamus sociabilis plumbeus*, in which either parent may abandon its mate. We describe the proximate factors controlling the occurrence of desertion and the sex of deserters. Ultimate factors affecting costs and benefits of mate desertion will be discussed in later papers, as are the demographic and environmental conditions that select for ambisexual mate desertion in this species (Beissinger 1986).

The snail kite is a neotropical hawk that nests in loose colonies and normally lays two to three eggs which hatch asynchronously (Nicholson 1926; Howell 1932; Chandler & Anderson 1974; Sykes 1979; Beissinger, in press b). Males assume the majority of nest-building duties, including courtship feeding, and both sexes participate in all

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aspects of parental care (Beissinger 1984, in press a). This species is best known for its almost exclusive diet of large freshwater *Pomacea* snails (Howell 1932; Snyder & Snyder 1969; Sykes & Kale 1974; Beissinger 1983; Takekawa & Beissinger 1983). The Florida population is endangered and highly unstable due to snail population fluctuations which result in parallel changes in kite numbers (Kushlan 1975; Beissinger & Takekawa 1983; Sykes 1983b). Under high water conditions the kite population expands rapidly, with pairs breeding nearly year-round in open marshes from central Florida south to the northern boundary of Everglades National Park. Under low water conditions breeding nearly ceases and the population crashes, as large areas of marsh dry out, forcing the birds to disperse widely (over the state) in search of food.

METHODS

Field studies were conducted from January through August in 1979, 1981 and 1982, in July and August 1980, and from March through June in 1983. Snail kite nesting activity was monitored throughout southern Florida wetlands used frequently by kites during the last decade, including Lake Okeechobee (Glades, Hendry, Okeechobee and Palm Beach Counties), State Water Conservation Area 3A (CA3A) (Dade and Broward Counties), and CA2 (Broward County). Sykes (1983a), Beissinger & Takekawa (1983) and Beissinger (1984) described these habitats and their use by kites during the study period.

Severe drought struck southern Florida in 1981. Nearly all wetlands traditionally used by kites were dry from May through August 1981, and again from April through May 1982, causing kites to disperse from the Everglades throughout the Florida peninsula. No successful nesting occurred in CA3A or CA2 in 1981–1982, or on Lake Okeechobee in 1982–1983. However, in 1982 two small breeding populations became established in locally favourable habitat in Osceola County, central Florida, Lakes Tohopekaliga (Toho) and Kissimmee (Beissinger & Takekawa 1983). In 1983, kites again nested in CA3A, after it had been flooded continuously for nearly a year, and a few nests were located in the adjoining northern section of Everglades National Park (Dade County) (Kushlan & Bass 1983).

During the 5 years of field studies, a total of 322 nests were found, 36 of which were studied intensively for mate desertion behaviour during approximately 2500 h of observations distributed throughout the nesting cycle. About one-fifth of these observations were made after mate desertion had occurred. Kite parents were observed for periods of 3–15 h from concealed locations 75–200 m from nest sites. Adults become dimorphic in plumage after 2 years of age (Beissinger, in press b) and the sexes of breeding birds are easily distinguishable. A nest was considered deserted when one parent stopped caring for the young and was no longer seen in the nesting area during 15–100 h of observation at a given nest on 3–10 different days. Because parents normally brought food to the nest 3–4·5 times/h during the periods just before and after mate desertion, our observation regime was more than sufficient to detect desertion.

To minimize the chances of causing desertion, we rarely visited actual nest sites more than once weekly and did not try to trap or band the adults (at nine of 36 nests studied for mate desertion behaviour, one parent had been colour-banded as a nestling years earlier). There was no evidence that our presence resulted in abnormal behaviour by parents at nests. Two nests (not included in Table I) found just after fledging were attended by only one parent, providing additional evidence that mate desertion occurred independently of our activities. Furthermore, it is unlikely that mortality accounted for most desertions because (1) desertion was common under good conditions when kite populations increased geometrically, but did not occur when poor conditions caused a severe population decline, and (2) the timing of desertion was sharply peaked close to fledging and adults did not disappear during incubation or shortly after hatching, which might have been expected with some frequency if these birds were simply dying. The one telemetered nesting bird that we were able to follow after its disappearance from the nest area did not die, but abandoned parental duties and re-mated.

At 18 nests, the frequency of snail deliveries to the young by each parent was monitored with binoculars and spotting telescopes. Observations were made twice weekly from hatching until nest sites were abandoned and parental care was nearly terminated. In 1979 and 1981, observation periods lasted from dawn until dusk (10–15 h), while mostly 5-h sample periods were used in 1982 and 1983. A detailed account of the daily observation periods at all nests is given in Beissinger (1984). For two to four nests that were watched frequently in each year, the farthest and closest distances travelled regularly from the nest site in search of food for the young were estimated to determine the foraging range.

Time–energy budgets were constructed for kites at two nests in 1979 and two in 1982 for which local topography made it possible to observe the behaviour of parents nearly continuously for 5-h, 8-h, or day-long sample periods. Days were grouped into pre- (2 weeks prior) and post-desertion (2–3 weeks after) periods for comparisons. Activities were timed to the nearest second. Categories of behaviour recorded are given in Beissinger (1983, 1984). Foraging bouts were categorized to reflect the recipient of the food item (self, young, unknown) based on the fate of the captured or subsequently captured food item. All time spent perching between captures during a foraging trip was included as foraging behaviour if the parent remained on the foraging ground and did not return to the nest area (less than 50 m from the nest site). All other activities were categorized as either general nesting activities (chasing conspecifics or potential predators, perching in the nest area, etc.) or lost (out of view to the observer). Daily energy expenditure (DEE) was calculated for time–activity budgets using an energetics model for wintering raptors (Koplin et al. 1980) adapted for use in the breeding season by substituting summer (breeding) estimates of existence metabolism (Kendeigh et al. 1977). A detailed account of the energetics model is developed elsewhere (Beissinger 1984).

At intervals of approximately 5 days, nestling growth was measured at 12 nests. Nestlings were weighed to the nearest g on Pesola spring scales, and culmen and wing chord lengths were measured (in mm) with calipers and rulers. Both weight and culmen length showed a sigmoid relationship with nestling age, but wing chord increased more linearly and was still increasing at fledging (Beissinger 1984). Wing chord was used to age nestlings of unknown hatching date.

In 1979, 11 nestlings from five nests where desertion occurred were fitted with back-pack, solar-powered radio transmitters. Eight non-breeding adult kites were trapped in 1981 and also fitted for telemetry in the same manner. Individuals were relocated by surface checks from an airboat and by airplane searches.

In 1981 and 1982, most kite nests were built in cat-tails (*Typha* sp.) and had to be placed in Chandler nest baskets to avoid failure due to structural weakening and collapse (Sykes & Chandler 1974; Chandler & Beissinger, unpublished data). The parents acclimated to these structures within an hour, and the baskets appeared to have no detectable effects on parental behaviour.

Data were analysed on the University of Michigan Amdahl 470V/8 computer using M.I.D.A.S. (Michigan Interactive Data Analysis System), BMDP Statistical Software, and by programs on a Hewlett–Packard 41-CV calculator. Means are reported with standard deviations (SD). Statistics follow Cox (1970), Remington & Schork (1970) and Conover (1980). Assumptions of normality and homoscedasticity of parametric models were examined by inspection of scatter plots, skewness and kurtosis coefficients, residual analyses and testing for homogeneity of variances. Non-parametric statistics were used when these assumptions were violated.

RESULTS

Who Deserts

Mate desertion occurred at 28 of 36 snail kite nests (Table I). Females deserted their mates 1·8 times as often as males. However, except for 1982, when a preponderance of females deserted, males and females deserted with nearly equal frequencies. For all years combined, the frequency of desertion by females was not significantly greater than that of males ($\chi^2 = 2{\cdot}24$, $P = 0{\cdot}13$).

Whether both mates ever desert a nest is difficult to determine because many nests are found empty without any evidence of the cause of failure or the sequence of events that occurred (Beissinger 1986). Many kite nests appeared to be abandoned by both mates before any eggs were laid ($N = 58$). Occasionally, kite nests were abandoned with eggs ($N = 4$) and very rarely with young ($N = 1$). These cases may not represent mate desertions, but were probably abandonments of reproductive bouts by both mates.

Effects of Food Availability on Mate Desertion

The occurrence of mate desertion was strongly correlated with variations in snail abundance and availability. We were unable to sample snail densities directly because the snails were normally too

Table I. Mate desertion and nesting success by snail kites in Florida

Year	Deserting parent: N(%)			Nest success	
	Male	Female	Neither	Young fledged ($\bar{X} \pm$ SD)	% Success (No. of nests)*
1979	3(37·5)	4(50·0)	1(12·5)	2·25±0·25	41(131)
1981	0(0·0)	0(0·0)	2(100·0)	1·00±0·00	0(12)
1982	2(16·7)	10(83·3)	0(0·0)	1·92±0·23	5(40)
1983	5(35·7)	4(28·6)	5(35·7)	2·07±0·12	21(48)
Total	10(27·8)	18(50·0)	8(22·2)	2·00±0·12	29(231)

*Successful nests are those that produced one or more young. Includes only nests found before hatching and those not placed into Chandler nest baskets (Chandler & Beissinger, unpublished data). Both successful nests of 1981 were in Chandler nest baskets, as were most successful nests of 1982.

thinly spread to yield reasonable estimates for the amount of effort expended. Instead, we used the distances travelled by kites from the nest in search of food as an inverse measure of snail abundance. Over the 4 years of study, there was a significant negative correlation between the percentage of nests that were deserted and the average maximum foraging range (Fig. 1).

Foraging ranges were largest during the severe drought of 1981, when snails were scarce and nesting success was lowest (Table I). Although no adults deserted at the only two successful nests of that year, each pair raised only one young: less than half the average number of young fledged from nests attended by single adults in other years. These were the only nests of one young not deserted during the study. Mate desertion was not observed at about one-third of the nests monitored in 1983, all of which nested in an area (CA3A) that had been dry for prolonged periods in 1981 and 1982 (Beissinger & Takekawa 1983). Judging from the relatively large foraging ranges of the kites and the paucity of snail egg clusters, snail populations were still depressed in this area in 1983. In 1979, a year of high food availability, the single case of non-desertion occurred late in the nesting season. All pairs studied in 1982 were in areas of obviously favourable food supplies, had very small foraging ranges and exhibited mate desertion.

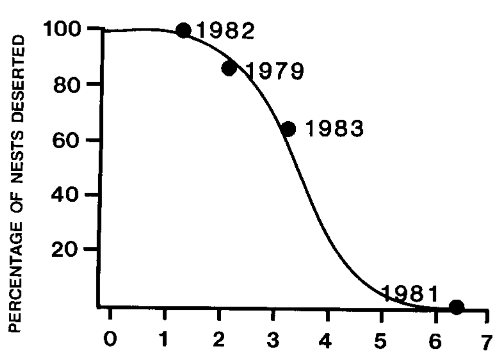

Figure. 1. The percentage of snail kite nests deserted by one mate in each year of study (P) in relation to the furthest distance from the nest regularly travelled by parents in search of snails (R). The foraging range maximum represents a mean for two nests in both 1979 and 1981, and four in both 1982 and 1983. A significant ($P = 0{\cdot}0003$) logistic regression $[P = 1/1 + e^{(1{\cdot}78*R - 6{\cdot}244)}]$ is fitted to the data.

If the abundance of snails is an important determinant of whether a parent can desert its mate, we might expect deserted nests to have higher snail delivery rates before desertion than nests that are not deserted. In comparing snail delivery rates between deserted and non-deserted nests, we chose to use the time period between weeks 3 and 7 when snail-delivery rates were nearly stable (Beissinger 1984). For broods of one and three, delivery rates before desertion were significantly greater at deserted nests than at nests that were not deserted (Table II). However, for broods of two, pre-desertion delivery rates were significantly lower at deserted nests than at non-deserted nests. After desertion, snail delivery rates at deserted nests were significantly greater for broods of one, significantly less for broods of two, and not significantly different for broods of three than at non-deserted nests.

Snail delivery rates do not necessarily account for variation in the size of snails delivered to the young. On the basis of shells we collected at nests and feeding perches, the average size of snails captured by kites did vary significantly between study areas (Beissinger 1984). However, when we recalculated snail delivery rates as an index of frequency times mean snail dry weight to account for differences in snail size in terms of energy value, results of the delivery rate–size index comparisons were nearly identical to those presented in Table II for frequency alone (Beissinger 1984).

Food availability might affect the growth rates of young, and parents might be less likely to desert young experiencing poor growth. Growth rate curves for weights of individual kite nestlings (Beissinger 1984) showed patterns similar to those of other altricial birds (Ricklefs 1968) with a linear increase (days 5–20) reaching an asymptote (days 21–27) and followed by a slight decline (greater than 27 days). Analysing only the period of linear growth, nestlings from male-deserted nests did not grow faster, but were heavier (had higher adjusted means) than female-deserted and non-deserted nestlings (Table III). However, this effect may not have been independent of brood size; broods of three, which were mostly deserted by males (see below), had higher adjusted means than broods of one or two. Overall, deserted nestlings did not grow faster and were not heavier than those that were not deserted. Similarly, nestlings from deserted nests did not grow faster ($P=0{\cdot}452$) and were not heavier ($P=0{\cdot}140$) than nestlings from non-deserted nests when the effects of brood size were incorporated into the ANCOVA model. However, nestlings from deserted nests tended to grow faster ($P=0{\cdot}089$) and were significantly heavier ($P=0{\cdot}038$) than non-deserted nestlings fledged during the 1981 drought.

The Timing of Desertion

In all cases but one, mate desertion occurred in the late nestling period or in the post-fledgling dependency period, stages when young no longer need to be brooded. On average, desertion occurred about a week before fledging, when the eldest chicks were 29 days old (range 15–53 days) and had reached an asymptotic weight (Beissinger 1984). At the only nest that was deserted before the chick was homeothermic, the tending male brooded and fed the lone nestling for over 10 days until the nest failed, apparently due to predation. Because the timing of desertion was very atypical at this nest, it is possible that the female died rather than deserted. Brood reduction prior to desertion, due to predation, weather, or possibly other factors, occurred at 40% of the deserted nests. Desertion followed within a week of brood reduction at 18% of the nests; however, the precise timing of brood reduction and desertion could not be determined at 22% of the nests.

Broods of one appeared to be deserted earlier ($22{\cdot}8\pm6{\cdot}2$ days after hatching, $N=4$) than broods of two ($27{\cdot}1\pm6{\cdot}1$ days, $N=7$) and broods of three ($34{\cdot}6\pm9{\cdot}9$ days, $N=7$; $F_{2,15}=3{\cdot}20$, $P=0{\cdot}07$). Because young hatch asynchronously, age differences of siblings can be nearly a week in larger broods. In part, larger broods may be deserted later because nestlings reach a peak probability of

Table II. Snail delivery rates by brood size for deserted ($N=13$) and non-deserted ($N=5$) nests

	Mean ± SD snails delivered per h (No. of observations)		
	Deserted nests		
Brood size	Before desertion	After desertion	Non-deserted nests
1	$1{\cdot}6\pm0{\cdot}5(6)^a$	$1{\cdot}6\pm0{\cdot}5(17)^a$	$0{\cdot}8\pm0{\cdot}4(12)^b$
2	$3{\cdot}2\pm1{\cdot}1(8)^a$	$3{\cdot}5\pm1{\cdot}0(12)^a$	$4{\cdot}4\pm1{\cdot}0(28)^b$
3	$4{\cdot}7\pm1{\cdot}4(28)^a$	$4{\cdot}3\pm1{\cdot}5(12)^{ab}$	$3{\cdot}5\pm1{\cdot}0(6)^b$

Daily observations of delivery rates at each nest from weeks 3–7 were pooled. Means for a given brood size with different superscripts differ from each other (Student's t-test, $P<0{\cdot}05$).

Table III. Analysis of covariance (ANCOVA) for nestling growth rates of weight in relation to desertion types, brood size and hatch order

Comparison	ANCOVA *P*-values: Slope	Adjusted means	Overall regression
Desertion types			
Male deserter vs. female deserter	0·426	0·001(↑)	0·005
Female deserter vs. neither	0·614	0·867	0·867
Male deserter vs. neither	0·195	0·002(↑)	0·004
Deserters vs. neither	0·331	0·118	0·185
Brood size			
One vs. two	0·345	0·367	0·426
One vs. three	0·558	0·004(↓)	0·014
Two vs. three	0·501	0·001(↓)	0·001
One vs. two vs three	0·574	0·002	0·001
Hatch order			
Old vs. mid	0·353	0·610	0·569
Old vs. young	0·791	0·829	0·943
Mid vs. young	0·316	0·520	0·490
Old vs. mid vs. young	0·506	0·773	0·757

Sample included three nests deserted by males, seven by females, and three not deserted. Arrows indicate the direction of significant differences in relation to the first parameter.

survival later in larger than in smaller broods (Fig. 2), perhaps due to larger age differentials.

Females deserted their mates and broods earlier than males: 25·5 ± 5·7 ($N=12$) days versus 36·2 ± 10·2 ($N=6$) days after hatching of first young ($U=10·0$, $P=0·01$). This difference may have been caused in part by a significant difference in the size of broods deserted by males and females ($\chi^2=7·68$, $P<0·02$; Fig. 3). Because females tended to desert smaller broods than males, they may have been able to leave them earlier.

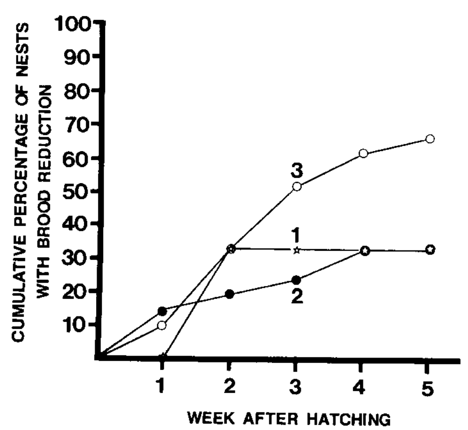

Figure 2. The cumulative percentage of nests experiencing brood reduction or failure in relation to time after hatching for nests with initial brood sizes of one ($N=3$), two ($N=21$) and three ($N=21$) young.

Post-desertion Behaviour of Deserters and Tenders

At nests where mate desertion occurred, the remaining adult (the tender) cared for the young

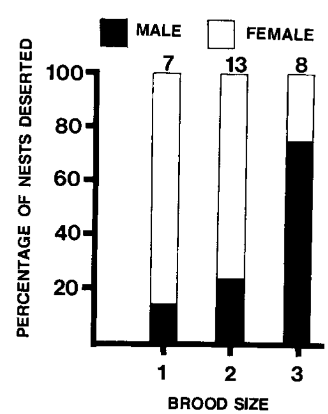

Figure. 3. The percentage of nests deserted by male and female snail kites in relation to brood size. Sample sizes are on top of each bar.

alone for 3–5 weeks until the latter reached independence. At 27 of 28 nests where mate desertion occurred, tenders successfully reared all young to independence. Furthermore, all 11 telemetered young from five deserted nests survived for over 1·5 years (the life of the transmitters) and at least one even nested at 1 year of age.

After desertion, tenders fed offspring at a rate equivalent to that of both parents before desertion (Table II). The effect of desertion on the tender's time–energy budget varied from relatively small to significant increases in time and energy expenditures (Table IV). At nest 79–3, the tending male spent over two-thirds of the daylight hours in foraging activities, while other tenders foraged during one-third to one-half of the observation periods. The lack of significant shifts in time–energy budgets of tenders was due primarily to brood reduction, alternative strategies employed by tenders (see Discussion), the effects of weather on kite activity (Carey 1985, personal observation), or small sample sizes. However, caring for the young was expensive, and tenders averaged energy expenditures of 460–720 kJ per day (Table IV), about 1·3–2·0 times the energy budget for non-breeding kites in Guyana (359 kJ; Beissinger 1983).

Little is known about the behaviour of deserters after desertion because of the difficulties in relocating them in the thousands of km^2 of Everglades habitat and the high mobility of kites (e.g. one male moved 160 km between successive nests in a season). The only deserting parent that we were able to follow after desertion was a telemetered female who deserted her mate, immediately re-paired, and was incubating eggs 2 weeks before her first mate finished caring for their first progeny.

DISCUSSION

To our knowledge, the snail kite is the only vertebrate for which the regular occurrence of mate desertion by either sex (ambisexual) has been documented (Table I). Male and female snail kites deserted with nearly equal frequency, except in 1982 when more females deserted. Most of the female-deserted nests in 1982 were on Lake Toho where there was a slightly skewed sex ratio; several unmated males were present during the early part of the nesting season and this may have encouraged females to desert. Skewed sex ratios have been shown to affect the occurrence of desertion (Keenleyside 1983), presumably by affecting the costs and benefits of desertion (Trivers 1972; Boucher 1977; Alexander & Borgia 1979).

Mate desertion occurred at nearly every nest during years of high snail abundance and favourable Everglades water levels. During these years, the only nest not deserted was initiated late in the nesting season. Because the option of re-pairing

Table IV. Time–activity and energy budgets of nest tenders for pre-/post-desertion periods

Time–energy component	Nest number: tender			
	K-8: Male	T-24: Male	79–1: Female	79–3: Male
N observation periods	2/2	3/5	2/5	4/4
Brood size	2/2	3/2	2/1	3/3
Time–activity budget				
% Time foraging:				
Self	15±8/11±4	11±9/11±4	9±2/23±12	21±9/21±9
Young	10±7/19±8	27±6/24±7	29±9/31±5	25±7/43±8**
Total	25±14/31±2	41±10/37±9	39±11/56±14	50±14/68±7*
% Time lost	43±50/54±14	9±2/5±3	3±4/7±6	10±7/6±2
DEE (kJ)				
Range	—	427–469/414–611	402–577/435–590	523–916/665–757
Mean	—	448±21/460±84	490±121/498±67	674±180/720±42

See Methods for definitions of foraging time categories and calculations of daily energy expenditure (DEE). No DEE was calculated for nest K-8 because the male was lost for a large portion of the time (see text). Statistical differences for within nest pre-/post-desertion comparisons using Student's *t*-test are $^{*}P<0{\cdot}10$ and $^{**}P<0{\cdot}05$.

and initiating a new nesting cycle did not exist for this nest, the potential benefits of desertion may have been less than those derived by continued parental investment. In years when snail availability was depressed by the effects of drought, mate desertion occurred less frequently or not at all. The size of kite foraging ranges, an inverse measure of snail abundance, was negatively correlated with the occurrence of desertion (Fig. 1), further supporting the relationship between food abundance and mate desertion.

However, the influence of snail abundance on the occurrence of mate desertion was demonstrated with only mixed success in comparisons of snail delivery rates and growth rates of young between deserted and non-deserted nests (Tables II, III). Before desertion, broods of two young were fed less frequently at nests that were later deserted than at those that were not, a result opposed to both our expectations and the findings for broods of one and three. However, the exceptional result for broods of two was not a function of low feeding rates for nests that were deserted, but of anomalously high rates for non-deserted nests. This suggests that factors other than food availability may have prevented desertion of some broods of two. For example, if desertion decisions are dependent on a parent knowing beforehand that unmated birds of the opposite sex are available in the general vicinity, an absence of unmated floaters in the specific range of a pair at the proper time in the nesting cycle could lead to a failure to desert, regardless of food availability. However, no good evidence exists to substantiate this hypothesis; in fact, near one of the non-deserted broods of two an apparently unmated male kite was seen giving courtship displays to the female of the pair for a brief period during the time when desertion normally occurs.

In any event, it is noteworthy that all three broods of two that were not deserted were from one area (CA3A) in one year (1983), and it seems possible that there might have been something peculiar about this region at the time. Growth rates followed a similar pattern: there was no significant difference between deserted and non-deserted nests (Table III) except when the 1983 data were not included. Other non-deserted broods were observed during the 1981 drought, and snail delivery rates and growth rates at these nests were significantly lower than at deserted nests. From these analyses, we can conclude that while desertion will not occur under poor food conditions, good food conditions may not always guarantee its occurrence, perhaps because factors other than food availability may also be important in eliciting this behaviour.

Females tended to desert small broods and males large ones (Fig. 3). We can offer no obvious explanation for this pattern. Parental investment theory (Trivers 1972; Dawkins & Carlisle 1976; Boucher 1977) predicts desertion by the sex with the greater potential gain by deserting and/or least cumulative investment (if past investments affect future reproductive efforts). Small broods do not imply low pre-hatching reproductive investment by female kites, because in nearly all cases small broods (less than three young) were the result of egg or offspring mortality rather than small clutch size. We can discern no effects of future potential benefits from deserting that would differ for males and females as a result of present brood size. However, the tendency of males and females to desert different-sized broods may be due to a shift over time of cumulative investment curves. Because male snail kites take the primary role in nest-building, courtship feeding and incubation, male investment usually exceeds female investment through hatching (Beissinger, in press a). And since males tend to contribute the bulk of food delivered shortly after hatching, reproductive investment by females may only have a chance to equal that of males once feeding rates rise after brooding is completed. Since larger broods require longer, more intense periods of parental care (Tables II, IV) and it may be risky to desert them early (Fig. 2), the probability of female investment exceeding male investment may be much greater for large broods than for small ones. Differences in parental investment may affect which snail kite parent does desert, because prior to desertion all deserting parents fed their young less frequently than did their mates (Beissinger 1984). However, it is not clear whether this difference was a causal factor in the desertion decision or a result of parents adjusting their investments in response to other factors, such as perceived opportunities to re-mate.

Mate desertion by snail kites usually occurs close to the time of fledging. Judging by the high success rate of single parents in raising their broods unaided, desertion occurs when the offspring are old enough for either parent to finish rearing them alone, as predicted in models by Maynard Smith (1977) and Grafen & Sibley (1978). The staggered timing of desertion for different brood sizes closely coincided with the onset of the period when each brood size was no longer susceptible to offspring mortality (Fig. 2). Desertion probably does not occur earlier because bi-parental care may be necessary from incubation through hatching and until brooding has been completed.

As a mating system, ambisexual mate desertion is a strategy that borders between classical monogamy and polygamy. Snail kite parents may be able to assess variation in food abundance in relation to the requirements of different brood sizes to determine when a monoparental threshold has been crossed so that one mate may safely desert, leaving the other to parent the brood to independence. Kites do not, however, adjust clutch size in relation to large year-to-year variations in food abundance (Beissinger 1986), but instead desert their mates if a monoparental threshold can be attained.

Mate desertion behaviour presumably evolved because, for deserters, the benefits of deserting were greater than the costs (Trivers 1972; Dawkins & Carlisle 1976; Boucher 1977; Maynard Smith 1977; Alexander & Borgia 1979). For snail kites, there are several presumed benefits of desertion for deserters. By deserting, deserters save 3–5 weeks of time that can be used to re-mate and increase their number of nesting attempts during the long breeding season, a period of up to 10 months of the year in Florida (Beissinger 1986). Evidence suggests that kites regularly attempt to raise more than one brood in a single breeding season in Florida. The potential for increased fitness afforded by desertion is demonstrated by a female who was incubating a second clutch 2 weeks before her mate finished caring for her first progeny. The long Florida breeding season offers individual kites a potential of three or conceivably four successive broods if they consistently desert and re-mate, but only two broods if they are consistent tenders. A second potential benefit of deserting is that by escaping parental duties, deserters are able to avoid the risks and physical deterioration associated with brood care, saving significant portions of reproductive effort (Table IV) that could be used later for reproduction or survivorship. Since kites in Florida have been known to reach 13 years of age (Beissinger 1986), such a saving of parental effort over a lifetime could be significant.

Deserters appear to incur no substantial costs by deserting. Deserters usually abandoned their mates without a reduction in reproductive output since tenders nearly always successfully reared all young to independence. Because snail kites are not territorial except under unusual conditions (Snyder & Snyder 1970), deserters do not forfeit future nesting opportunities or incur the costs of establishing a new territory after desertion. Locating and courting a new mate might be more costly to a deserter than waiting and re-mating with its present mate. But individuals that hesitate to desert risk being deserted themselves, which probably results in even greater costs.

By remaining and caring for the young alone, tenders may incur substantial costs. They lose 3–5 weeks of time that could be used for re-nesting, about one-quarter of the period required for one nesting cycle. Tenders may experience increased energy expenditures after being deserted (Table IV). Such a parental investment by a tender accumulated over the post-desertion period may represent one-quarter of the cumulative reproductive investment of a nesting attempt (Beissinger 1984) and accrued over several reproductive bouts would be a significant portion of lifetime reproductive effort.

Tenders pursued two alternative strategies that mitigated the cost of being deserted. One strategy, nutrient and energy replenishment, was exemplified by the female tender at nest 79–1. While committed to caring for a single nestling alone for 5 weeks, this female increased the amount of time spent foraging for herself over 2·5 times after being deserted (Table IV). This was probably a mechanism for her to replenish nutrient and energy reserves in anticipation of beginning a new nesting cycle, which she did immediately after terminating parental care. This strategy is more likely to be used by tenders caring for small broods, since larger broods require more time for provisioning the young (Table IV). In the second strategy, clutch overlap (Burley 1980), tenders attempted to secure a new mate while still provisioning the young. This behaviour was observed twice (both instances were males) but neither attempt was successful. Successful clutch overlap by tenders probably occurs very rarely because it would require high snail abundance so that male tenders could feed both the young and a prospective mate (Beissinger, in press a), or female tenders could feed young without expending much of the energy needed for egg production. Also, a mate and a new nest site must be available near the old one. Female tenders probably rarely use this strategy because during courtship and egg laying they minimized energy expenditures and received considerable food from their mates, presumably to allow rapid production of eggs (Beissinger, in press a).

For deserted kite parents of either sex, there is no viable alternative strategy to tending their offspring because desertion occurs relatively late in the nesting cycle (Trivers' cruel bind, 1972), when the probability of successfully completing brood rearing is high, while the likelihood of being successful in a new nesting attempt is low (Table I). Because both parents are equally able to rear the young alone, either sex can desert at the appropriate moment. Birds may be the most likely vertebrates to exhibit ambisexual mate desertion since parental duties are often shared throughout a nesting cycle (Lack 1968; Oring 1982). Because it is difficult to detect desertion late in a reproductive bout, ambisexual mate desertion may be easily overlooked and could be occurring in other vertebrates where both parents appear to care for the young.

ACKNOWLEDGMENTS

Financial support was provided by the United States Fish and Wildlife Service (including Cooperative Agreement No. 80–1012 from the Endangered Species Ecology Section of Patuxtent Wildlife Research Center). Additional support was received from The University of Michigan, Frank M. Chapman Memorial Fund, National Audubon Society, National Wildlife Federation and Everglades National Park. Owen Ballow, Rod and Noel Chandler, Gary Falxa, Carolyn Glynn, David Jickling, Margaret Lansing, Steven Manz, Margaret Moore, Lisa Pakula, Margaret Reeves, Helen Snyder and Margaret Stein assisted with field work. Assistance with data analysis by Rob Kushler is gratefully acknowledged. For reviews of various drafts of this work, we thank Richard Alexander, Gary Belovsky, Scott Derrickson, Ron Drobney, Stephen Emlen, Gary Fowler, Bobbi Low, Douglas Mock, Eugene Morton, George Powell, Charles Snowden, Jared Verner and Rod Walton.

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(*Received 19 February 1986; revised 11 March 1986; MS. number: A4579*)

Anim. Behav., 1987, **35**, 488–506

The closed environment of the fig receptacle and its influence on male conflict in the Old World fig wasp, *Philotrypesis pilosa*

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Abstract. The influence of the environment on the fighting behaviour and susceptibility to injury of male *Phylotrypesis pilosa*, a parasitic fig wasp, was examined with reference to a recent model of contest competition. The model was extended by deriving an expression for the overall rate at which contest costs accumulate during resource exploitation. Predictions were then made about the cost and frequency of fights, and about the overall cost of fighting with regard to variations both in the density of males and females and in the ratio of females to male competitors. The cost of fighting was estimated from the length and frequency of fights and by the extent of male injuries. The overall cost of conflict was highest at an intermediate density of males, as predicted. The overall cost also rose as the density of females increased but, unexpectedly, did not peak at an intermediate female density. A predicted relationship between fighting cost and the ratio of female number to male competitor number was also missing. These discrepancies were associated with a difference in the actual and assumed form of sperm utilization that followed mating, and with the surprising ability of males to alternate rapidly between guarding and exploratory behaviours. The data give no indication that males are either reducing their levels of aggression in fights with relatives, or increasing them to establish dominance when encountering the same competitor repeatedly.

An odd combination of fighting and harmony is found amongst animals that associate closely within social groups or small isolated subpopulations. Compare the corporate intimacies of naked mole-rats (*Heterocephalus glaber*, Jarvis 1981) with the widespread infanticide among ground squirrels (Sherman 1981); fratricide among nest-mates of kittiwakes or cattle egrets, *Ardeola ibis* (Braun & Hunt 1983; Fujioka 1985) with the filial help given at nests of bee-eaters or tropical wrens (Emlen 1981; Rabenold 1985); and queen fights with sister altruism in many social Hymenoptera (Wilson 1971; Hamilton 1972). The same peculiar divergence in behaviour occurs among fig wasps where species with armoured males and lethal combat can share their fig receptacle (syconium) with species showing no signs of male aggression, either in their behaviour or morphology (Hamilton 1979). Ultimately, this mixture of amicable and aggressive behaviours is induced by physical and social environments which impinge strongly on group-living animals. Thus, Hamilton (1979) suggested that fighting between fig wasps can be particularly damaging because the wingless males cannot leave one syconium to find another. Clearly, when opportunities elsewhere are hard to come by, it is worth investing more in procuring a near-by contested resource. Hamilton also proposed that a high level of relatedness inside a syconium was a compelling constraint on fighting. Then again, it has been suggested that the very factors that bring close relatives together often keep the selfsame individuals together, providing opportunity for the formation of dominance–subordinate relations. Dominance fights tend to be particularly violent since much is at stake (Geist 1971; Murray & Gerrard 1984).

So many other social and ecological parameters potentially affect fighting behaviour that it becomes difficult to determine their individual contributions. One way round this problem is to redirect attention from variables describing the external environment (where the focus is on spatial or temporal distributions of resources and the structure of populations) toward variables that describe the interaction between the animal and its surroundings (here the focus is on an individual's

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