Mate desertion and reproductive effort in the snail kite

STEVEN R. BEISSINGER*

School of Natural Resources, University of Michigan, Ann Arbor, Michigan 48109-1115, U.S.A.

Abstract. Trivers' (1972) mate desertion model was tested by relating measures of reproductive effort for snail kites, *Rostrhamus sociabilis*, to the sex of the deserting parent. Deserters incubated, brooded and chased potential predators as frequently as did non-deserting mates. Only provisioning of nestlings differed significantly between deserters and their mates, correctly predicting which individual deserted at all nests. Reduced feeding by deserters became established within the first 2 weeks after hatching. Cluster analysis sorted three of four nests deserted by males into one cluster and the other male-deserted nest, which was deserted later in the nesting cycle than all others, clustered with non-deserting nests. Daily energy expenditure was measured throughout the nesting cycle to estimate reproductive effort: at three of four nests, deserters expended less energy than their mates prior to desertion, but in one case, cumulative energy investments did not predict which mate should have deserted. Differences in reproductive effort between mates may have predicted which mate deserted because (1) cumulative reproductive effort is a good indicator of the costs and benefits of desertion, and (2) deserters may assess the potential for deserting by testing their mate's abilities to care for the young. The influence of other factors affecting the costs and benefits of mate desertion decisions by snail kite parents is also discussed.

Trivers (1972) recognized that when the disparity of reproductive effort between the sexes was large, sexual selection could result in different strategies by the sexes to optimize the lifetime expenditure of reproductive effort. A mating system may then evolve as a function of the relative and temporal disparity in reproductive effort invested by the sexes. Trivers' (1972) hypothesis predicts that the sex whose cumulative investment is exceeded by its mate should be more tempted to desert because the deserter loses less than its partner if no young are raised. However, desertion decisions should be based on the expected costs and benefits (in terms of future reproductive success) of desertion to the deserter, regardless of past investments unless they affect future reproductive efforts (Dawkins & Carlisle 1976; Boucher 1977). Thus, Trivers' hypothesis can be restated as: an individual investing less reproductive effort than its mate should desert because it has less to lose if the current bout fails, since in future bouts a deserter expects to expend less reproductive effort than its mate to accrue the

same reproductive benefit (reach the same point as when it deserted in the present bout). The tendency to desert, however, will depend not only on the differences in reproductive effort between mates, but also on other factors affecting the costs and benefits of desertion (Boucher 1977; Maynard Smith 1977; Alexander & Borgia 1979): (1) the potential for increased or decreased reproductive success by deserting, (2) confidence in paternity or maternity, and (3) age as it relates to both reproductive value (Fisher 1930) and experience.

Studies testing Trivers' mate desertion model (sometimes denoted as parental investment theory) are rare. The conditions favouring mate desertion have been examined using game theory and graphical models (Maynard Smith 1977, 1982; Grafen & Sibly 1978), but it is not clear from field studies whether animals make decisions based on past investments rather than future benefits (Robertson & Biermann 1979; Weatherhead 1979; Andersson et al. 1980; Dawkins & Brockmann 1980; Coleman et al. 1985). For several reasons no studies have convincingly related reproductive effort to specific mating systems. First, mate desertion, if it occurs, is usually sex-specific (Kleiman 1977; Ridley 1978; Perrone & Zaret 1979; Wells 1981; Oring 1982); since only one sex deserts, the sex of the deserter can rarely be manipulated experimentally. Second, the distribution of reproductive effort between the

* Present address: Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, D.C. 20008, U.S.A. (to which correspondence should be addressed) and Department of Wildlife and Range Sciences, School of Forest Resources and Conservation, University of Florida, Gainseville, Florida 32611, U.S.A.

sexes is not easily manipulated. However, the total effort in a reproductive bout and the potential benefits of desertion to the deserter can be controlled by manipulating the number of offspring and operational sex ratios (Robertson & Biermann 1979; Patterson et al. 1980; Keenleyside 1983). Third, it is not always clear which behaviours constitute reproductive effort, and in what units it should be measured. Most studies have estimated reproductive effort using ratios of caloric values of eggs to body mass for the purpose of comparisons between species (e.g. Tinkle 1969; Tinkle & Hadley 1975; Congdon et al. 1983), but this technique cannot be used for intraspecific sex-related comparisons. However, the caloric expenditures of an individual during a reproductive bout can be estimated using reproductive bioenergetics and time–energy budgets (Hirschfield & Tinkle 1975; Walsberg 1983). Assessing risks associated with reproduction, the other component of reproductive effort, may be accomplished to some degree by using subjective indices for the most risky behaviours associated with reproduction (e.g. chasing potential predators or conspecifics; Andersson et al. 1980). But for many common behaviours like foraging or incubating, risk is difficult to assess. Although no method presently exists to integrate risk and energy into one unit of measurement of reproductive effort, risk indices can be used to augment observed energy expenditures as an estimate of investment trends.

Despite these problems, Trivers' mate desertion hypothesis has been examined by relating indices of reproductive effort to desertion decisions by monogamous mates (Røskaft 1983; Anderson 1984). A more definitive test for Trivers' model of mate desertion would be to examine reproductive effort or its correlates for breeding individuals of pairs in a species where either sex will desert. The unusual mating system of the snail kite, *Rostrhamus sociabilis*, offers this opportunity.

Snail kites are medium-sized raptors noted for their specialized habit of feeding almost solely on freshwater snails of the genus *Pomacea* (Howell 1932; Snyder & Snyder 1969; Sykes & Kale 1974; Beissinger, in press), and for their novel mating system of ambisexual mate desertion (Beissinger 1984; Beissinger & Snyder 1987). If snails are sufficiently abundant, mate desertion may occur in the midst of a reproductive bout when the young are 3–6 weeks old. Males and females desert with

similar frequency. Offspring mortality, however, rarely occurs after desertion. Deserters can escape parental duties or re-nest during the breeding season (a period of up to 10 months in Florida), while non-deserting mates (tenders) must finish rearing the young alone for 3–5 weeks.

In this paper, I test predictions about mate desertion in the snail kite based on Trivers' (1972) model. If a disparity in reproductive effort influences which parent deserts at a given nest, then (1) deserters should expend less energy and take fewer risks in reproduction than their mates; (2) correlates of reproductive effort (behaviours such as incubation and feeding of the young) should also be performed less frequently by deserters than by tenders; and (3) ambisexual mate-desertion systems should show high variability among nests with regard to the sex that performs parental behaviour. The following predictions, based on the factors that affect the costs and benefits of mate desertion, can also be made: a deserter is more likely to be the individual that has the first opportunity to re-mate, is less confident of its paternity or maternity, and is older and more experienced. However, none of these factors could be quantified for all nesting kites because (1) plumage dimorphism does not occur until after 2 years of age (Beissinger, in press), so operational sex ratios could not be measured to assess mate availability; (2) tissues required for electrophoretic exclusion analyses were not obtained because the Florida kite population is endangered, and trapping activities might have affected mate desertion behaviour or nesting success; and (3) the age of breeding birds could not be determined from plumage characteristics, and only a quarter of the parents had been banded as nestlings. However, generalizations about the probable influence of these factors on the sex of deserting snail kite parents are discussed from qualitative observations.

METHODS

Behavioural Studies

From 1979 to 1983, field studies were conducted in southern Florida. See Beissinger & Takekawa (1983), Beissinger (1984, 1986) and Beissinger & Snyder (1987) for specific dates of study, locations of study areas and environmental conditions for

each year. Observations of kite nesting behaviour were made in all years except 1980.

To sample correlates of reproductive effort, observations were made once or twice weekly at 13 nests from pair formation or incubation until the young were independent, and at five nests from hatching until the young were independent. Nesting pairs were observed with binoculars and spotting scopes from a canoe, airboat, an observation tower, or tree blind from 75 to 200 m away from the nest site. In 1979 and 1981, observation periods lasted from dawn until dusk (10–15 h) while mostly 5-h sample periods (range 3–8 h) were used in 1982 and 1983. At most nests, females appeared to assume the majority of nighttime incubation duties, although males sometimes incubated overnight. Reproductive effort was assumed to be unaffected by nocturnal activities because the caloric cost of incubation may not be greater than resting metabolic costs (Walsberg & King 1978; Gessaman & Findell 1979; Vleck 1981; Walsberg 1983; Grant 1984), and incubating is probably not riskier to a parent than is roosting near a nest by the other parent.

Measures of reproductive effort were examined for each of the following periods of the nest cycle: Prezygotic (from pair formation until egg laying was complete; see Beissinger 1987 for these results); Incubation, Brooding (from hatching until a parent no longer brooded the young), Post-brooding (from the end of Brooding until mate desertion occurred) and Monoparental Care (after the occurrence of mate desertion). Nest observations totalled 2295 h: 202 h during Prezygotic, 598 h during Incubation, 401 h during Brooding, 764 h during Post-brooding and 330 h during Monoparental Care. The following correlates of parental effort were measured at each nest: (1) the percentage of time males incubated as a proportion of the total time both mates incubated, and incubation bout duration (min) of each parent; (2) the percentage of time males brooded young as a proportion of the total time both mates brooded, and brooding bout length (min) of each parent; (3) the percentage of time and bout duration (min) during a sample that the eggs were uncovered or the young were not brooded; (4) the number of snails delivered to the young by each parent, expressed as the percentage contributed by males during Brooding, Post-brooding, and during both periods combined (before desertion); and (5) the number of aggressive chases of predators or conspecifics by each parent,

expressed as the percentage of the total number of chases made by males.

A two-stage index was developed to assess risks incurred by each parent during nest-defence chases: (1) the length of the chase was designated as short (less than 30 s) or long (greater than 30 s); and (2) the risk of potential injury or mortality to the chasing kite inflicted by contact with the bird being chased (assessed on the basis of relative body size and morphology) was rated as Low, Medium, or High. Low risk included chases of small birds such as red-winged blackbirds, *Agelaius phoeniceus*, and boat-tailed grackles, *Quiscalus major*; medium-risk chases included chases of other snail kites, egrets and herons, turkey vultures, *Cathartes aura*, and fish crows, *Corvus ossifragus*; and high risk included chases of larger birds of prey such as bald eagles, *Haliaeetus leucocephalus*, and northern harriers, *Circus cyaneus*. For each parent, each index (1 and 2 above) was totalled for all chases, summed together to obtain an estimate of total risk incurred, and then expressed as the percentage per reproductive bout taken by males. Average risk per chase incurred by males and females were also used in behavioural analyses. Nests where too few chases (less than four) were observed were excluded from analysis.

In 1979 and 1982, time–activity budgets were constructed from detailed observations at four nests. Observations were made once or twice weekly in the same manner as described above; however, the behaviour of the parents was observed nearly continuously for 5-h, 8-h, or day-long (10–15-h) sample periods. Activities were timed to the nearest 1 s. Behaviour was categorized as (1) incubating, (2) brooding, (3) foraging (see Beissinger 1983 and Beissinger & Snyder 1987 for definitions of behaviours), (4) chasing, (5) perching, (6) nest building, (7) display flights, (8) flying (to change locations), and (9) lost (out of the observer's view). For each parent, the percentage of time spent in each behaviour was recalculated as the percentage of the sample excluding lost time. Individuals were rarely lost for more than 10% of an observation period, with the notable exception of male K-8 late in the nesting cycle, when he tried to secure a new mate away from the nest area. On days when male K-8 was lost for more than 40% of the time, I did not exclude lost time from the calculations but considered male K-8's investments to include only those behaviours that I viewed.

Energetics Model and Measurement of Reproductive Effort

Daily energy expenditure was calculated from time–activity budgets for a 13-h photoperiod, the average daylength during the kite nesting season in Florida (range 10–15 h). I adapted an energetics model for wintering raptors (Koplin et al. 1980) for use in the breeding season by (1) substituting Kendeigh's (Kendeigh et al. 1977) summer (breeding) estimates of existence metabolism (equations 5.28 and 5.35) for wintering equations (3 and 4) of Koplin et al. (1980), and (2) using Kendeigh et al.'s (1977) summer estimates of standard metabolic rate (equations 5.8 and 5.15) instead of the wintering equations (6 and 7) of Koplin et al. (1980). Average daily ambient air temperature was calculated from hourly readings during observation periods. Average nightly ambient air temperature was estimated using climatological data for local stations from the U.S. Environmental Data and Information Center, Ashville, North Carolina. Body mass was assumed to be 367·6 g (Beissinger 1983) for both males and females, since sexual size dimorphism in snail kites is extremely small (Snyder & Wiley 1976).

My daily energy expenditure model uses existence metabolism (Kendeigh et al. 1977), which distinguishes only between flight and non-flight activities in terms of metabolic costs. Lumping behaviours into these two energetic cost categories is justified because the cost of flight is six–nine times greater than that of other types of behaviour (Aschoff & Pohl 1970; Koplin et al. 1980; Walsberg 1983), and there is little variation between the estimates of metabolic costs of non-flight behaviour such as walking, perching, or nest attendance (Mugaas & King 1981). Furthermore, the costs of some non-flight activities are not well known. Existence metabolism integrates the costs of basal metabolism, temperature regulation, incubation, moulting, feeding and low-level cage locomotion activity into one estimate (Kendeigh et al. 1977), eliminating the assignment of arbitrary costs to each non-flight activity. Field tests of similar models have verified their utility (Koplin et al. 1980; Weathers et al. 1984; Williams & Nagy 1984).

In this study, reproductive effort is defined as all energy expended during a nesting cycle that is devoted to reproduction, and excludes energy expended during reproduction for non-reproductive purposes. But it can be difficult to classify whether or not a behaviour contributes to successful reproduction. For example, perching near the nest site may be a form of guarding against potential predators, simply loafing, or both. For animals with extended periods of parental care, the costs of reproduction (mating effort = ME and parental effort = PE, after Low 1978) have associated maintenance costs (M) if organisms are to survive to continue caring for the young. For instance, a parent bird feeding three nestlings may need to increase its own food intake to compensate for an increased daily energy expenditure. This leads to the following model for reproductive effort (RE)

$$RE = (ME + M_{ME}) + (PE + M_{PE})$$

Because time–activity observations used to estimate RE may also include somatic effort (SE), the following model of a field measurement of daily energy expenditure (DEE) as it relates to reproductive effort emerges

$$DEE = (ME + M_{ME}) + (PE + M_{PE}) + SE$$

so that daily RE = DEE − SE.

Estimating SE is not easily accomplished. During the Prezygotic period, SE was assumed to be small since nearly all activities observed were related to reproduction, and males and females may have barely met their maintenance requirements for energy intake (Beissinger 1984, 1987). Somatic effort could not be estimated for the remainder of the nesting cycle because nearly all parental behaviour, except when a parent forages for itself, could be interpreted as contributing directly to reproductive success. Instead, a minimum estimate of DEE (RE_{min}), excluding all energy invested in foraging when a parent ingested a snail itself (M_{PE}), was calculated in addition to a maximum estimate (RE_{max}) equivalent to DEE. Because estimates of RE_{min} underestimate RE by M, actual values of RE can be expected to lie between RE_{min} and RE_{max}. For hypothesis testing, actual values of RE are less important than the relative difference within each nesting pair.

Cumulative RE investment curves (RE_{min} and RE_{max}) were generated for each mate by using weekly means coupled with means from the appropriate model for the Prezygotic period (Beissinger 1987). For the occasional weeks where DEE was

Table I. Comparison of parental effort correlates at nests where males, females, and neither parent deserted

	Deserting parent: $\bar{X} \pm$ SEM (N)			Comparison†	
Parental effort correlate	Male	Female	Neither	Male versus female	Deserted versus non-deserted
Incubation					
% By male	60±9 (2)	50±9 (8)	41±2 (2)	NS	NS
% Uncovered	0±0 (2)	3±1 (8)	0±0 (2)	(*)	NS
Male bout length (min)	62±3 (2)	52±8 (8)	62±13 (2)	NS	NS
Female bout length (min)	55±8 (2)	42±4 (6)	68±0 (2)	NS	(*)
Uncovered bout length (min)	0±0 (2)	5±1 (8)	2 (1)	(*)	NS
Brooding					
% By male	26±1 (3)	36±1 (8)	22±1 (4)	NS	(NS)
% Uncovered	45±24 (3)	12±3 (8)	38±6 (4)	(NS)	NS
Male bout length (min)	15±6 (3)	19±2 (8)	21±2 (4)	NS	NS
Female bout length (min)	25±2 (3)	30±6 (8)	34±8 (4)	NS	NS
Uncovered bout length (min)	24±13 (3)	5±1 (8)	23±9 (4)	(*)	NS
Feeding					
% By male during Brooding	45±4 (4)	66±5 (8)	63±7 (5)	*	NS
% By male during Post-brooding	41±5 (4)	62±5 (8)	50±4 (5)	*	NS
% By male before desertion	42±4 (4)	65±4 (9)	53±5 (5)	**	NS
Chases and risk					
% Chases by male	63±10 (3)	50±4 (7)	66±23 (3)	NS	(NS)
% Risk by male	63±12 (3)	50±4 (7)	64±24 (3)	NS	(NS)
Mean male risk	2·0±0·1 (3)	2·0±0·2 (7)	2·0±0·1 (3)	NS	NS
Mean female risk	2·0±0·5 (3)	1·9±0·1 (7)	2·3±0·2 (2)	(NS)	NS

† Student *t*-test (or Mann–Whitney U) significance values are NS $P > 0.05$; * $P < 0.05$; ** $P < 0.01$.

not measured, it was estimated from means of preceding or subsequent values in the same period of the nesting cycle.

Statistical Analysis

Statistical analyses were conducted on the University of Michigan Amdahl 470v/8 computer. Assumptions of normality and homoscedasticity of parametric models were examined and non-parametric statistics were used when these assumptions were violated. Statistical tests were interpreted cautiously because, in many analyses, small sample sizes could lead to Type II errors. A single-linkage, Q-type cluster analysis was performed using all of the behavioural correlates of reproductive effort to assign each nest to a cluster based on Euclidean distances using SYSTAT microcomputer programs. Unless otherwise stated, means $(\bar{X})$ are reported with standard deviations (SD) and sample sizes (N). When standard errors (SEM) were given instead of SD, these were noted.

RESULTS

Behavioural Correlates of Parental Effort in Deserting Kites

Temporal patterns of incubation and feeding showed much variation among nests in the relative contribution of each parent (Beissinger 1984). Day-to-day variation in parental-care roles by the sexes was high at some nests and low at others. At some nests, investment by the deserter increased or decreased just before desertion, while at others no pattern was discernible.

Means of parental effort correlates at each nest are compared among nests where either males, females, or neither parent deserted (Table I), and the variation among and within nests in the three major parental activities is shown in Fig. 1. The role of the sexes in incubation duties was highly varied: seven nests were incubated primarily by males (more than 59% of the time), four primarily by females (more than 59% of the time), and duties were shared nearly equally in the other seven (range = 41–59%; sample includes six nests not
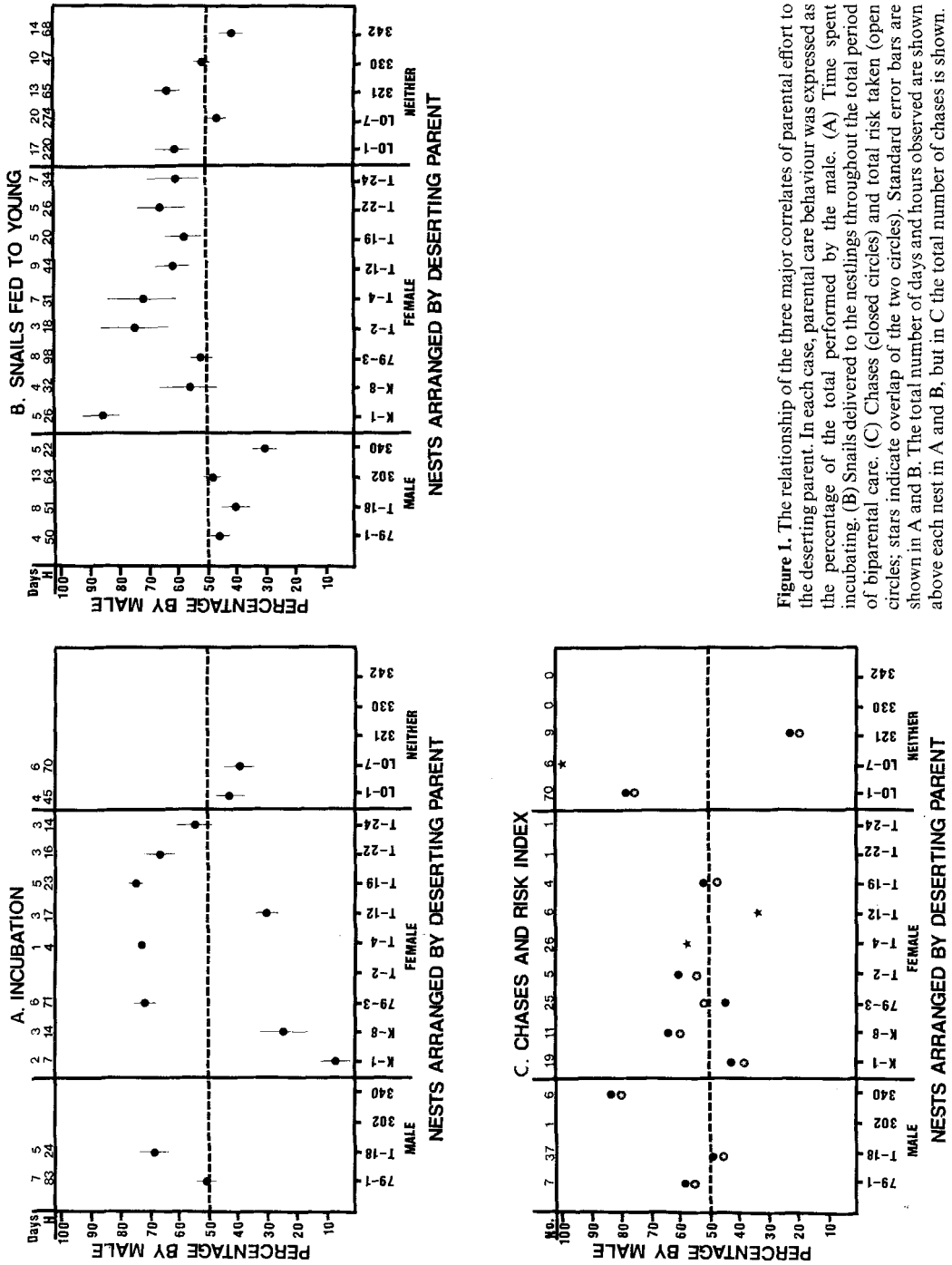
Figure 1. The relationship of the three major correlates of parental effort to the deserting parent. In each case, parental care behaviour was expressed as the percentage of the total performed by the male. (A) Time spent incubating. (B) Snails delivered to the nestlings throughout the total period of biparental care. (C) Chases (closed circles) and total risk taken (open circles; stars indicate overlap of the two circles). Standard error bars are shown in A and B. The total number of days and hours observed are shown above each nest in A and B, but in C the total number of chases is shown.
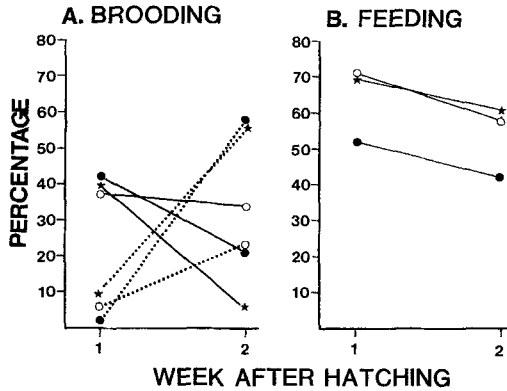
A. BROODING   B. FEEDING

WEEK AFTER HATCHING

Figure 2. Parental roles during the first 2 weeks after hatching. (A) The percentage of time nests were left unattended during brooding (dotted line), and the percentage of time males brooded young as a proportion of the total time both mates brooded (solid line) at nests eventually deserted by males (closed circles) or females (open circles), and for pairs where neither parent deserted (stars). (B) The percentage of snails delivered to nestlings by males, with symbols for desertion types as in A.
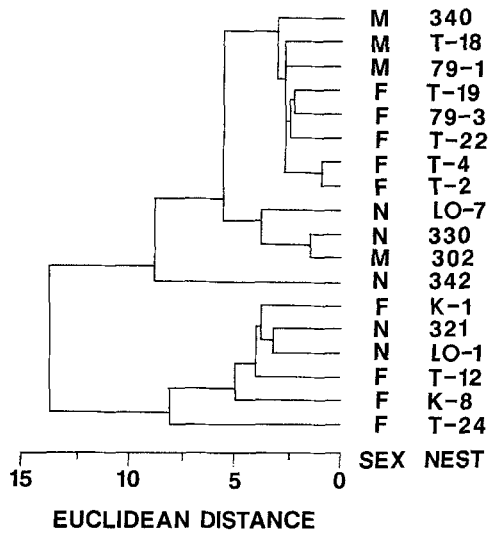

EUCLIDEAN DISTANCE

Figure 3. A cluster dendrogram, based on the Euclidean distances of 17 correlates of parental effort (Table I), depicting the relationships among 18 nests where either male (M), female (F), or neither (N) parent deserted their mate.

shown in Fig. 1 because they failed before mate desertion occurred). Tenders and deserters did not differ in the percentage of daylight hours spent

incubating or in the length of incubation bouts (Table I). Nests deserted by females were left uncovered during incubation for significantly more time and for longer periods than nests that were deserted by males. The only incubation variable that differed significantly between deserted and non-deserted nests was the length of bouts by females; bouts were significantly longer at nests that were not deserted than those that were deserted. However, the reason for this difference is not known.

Females brooded more often and for longer than males at all nests (Beissinger 1984). The amount of time a nest was brooded decreased significantly between weeks 1 and 2 after hatching (Fig. 2A) as the young became more homoiothermic (paired t-test, $N = 10$, $P < 0.002$). The only variable associated with brooding that differed among deserted nests was the length of time that the young were left unbrooded which was higher at nests where males deserted than at nests where females deserted (Table I). This was primarily a result of temporal changes in brooding duties (Fig 2A): males brooded at similar rates at both male- and female-deserted nests during week 1; but during week 2, male contribution to brooding declined by 50% at nests later deserted by males, but remained unchanged at nests later deserted by females. Non-deserted nests could not be distinguished from deserted nests on the basis of brooding variables. Non-deserted nests showed brooding patterns similar to those at male-deserted nests except that males brooded even less, probably because they spent more time foraging (see below).

The most important correlate of parental effort for discriminating nests in which males versus females deserted was the relative contribution of each parent to provisioning the young. Deserters provided snails for nestlings significantly less frequently than tenders during Brooding, Post-brooding, and for both periods combined (Table I). This pattern held for all nests that were deserted (Fig. 1B). In comparison, parents contributed more equally to provisioning the young in nests that were not deserted after brooding ceased. Lower participation by deserters in feeding the young may become established during the first 2 weeks after hatching (Fig. 2B). The percentage of snails delivered to the young by males was nearly 20% lower at male-deserted nests than at non-deserted and female-deserted nests. Thus, shortly after hatching, deserters may begin to establish a pattern of

Table II. Correlation matrix of parental effort correlates

| Parental effort correlate	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Incubation																
1. % By male																
2. Male bout length	0·84**															
3. Female bout length	−0·33	0·04														
4. % Uncovered	−0·42	−0·33	−0·59													
5. Uncovered bout length	−0·45	−0·40	−0·63**	0·86**												
Brooding																
6. % Uncovered	0·15	0·54	0·43	−0·15	−0·15											
7. % By male	0·58*	0·39	−0·07	−0·27	−0·34	−0·58*										
8. Male bout length	0·32	0·67*	0·42	0·06	−0·17	−0·32	0·48									
9. Female bout length	−0·31	−0·05	0·01	−0·01	0·03	−0·05	−0·42	0·03								
10. Uncovered bout length	0·03	0·39	0·66*	−0·36	−0·39	0·83**	−0·49	−0·27	0·04							
Feeding																
11. % By male during brooding	−0·48	−0·59*	−0·24	0·50	0·28	0·27	−0·10	−0·19	−0·02	−0·22						
12. % By male during post-brooding	0·06	−0·13	0·03	0·05	0·12	−0·32	0·57*	0·08	−0·52	−0·22	0·35					
13. % By male before deserting	−0·38	−0·57	−0·28	0·52	0·36	−0·51	0·20	−0·06	−0·24	−0·34	0·84**	0·71**				
Chases																
14. % Chases by male	−0·20	0·06	0·44	−0·23	−0·24	0·30	−0·38	0·33	0·55	0·60*	−0·37	−0·40	−0·40			
15. % Risk by male	−0·16	0·11	0·42	−0·21	−0·21	0·33	−0·37	0·36	0·54	0·60*	−0·42	−0·38	−0·42	0·99**		
16. Mean male risk	0·83**	0·81**	−0·12	−0·25	−0·22	0·26	0·49	0·47	−0·38	0·15	−0·67*	−0·12	−0·53	−0·06	0·01	
17. Mean female risk	0·20	0·09	−0·01	−0·26	−0·31	0·13	−0·38	−0·21	0·07	0·38	0·19	−0·16	0·06	−0·01	−0·06	−0·26

* $P < 0.05$; ** $P < 0.01$.
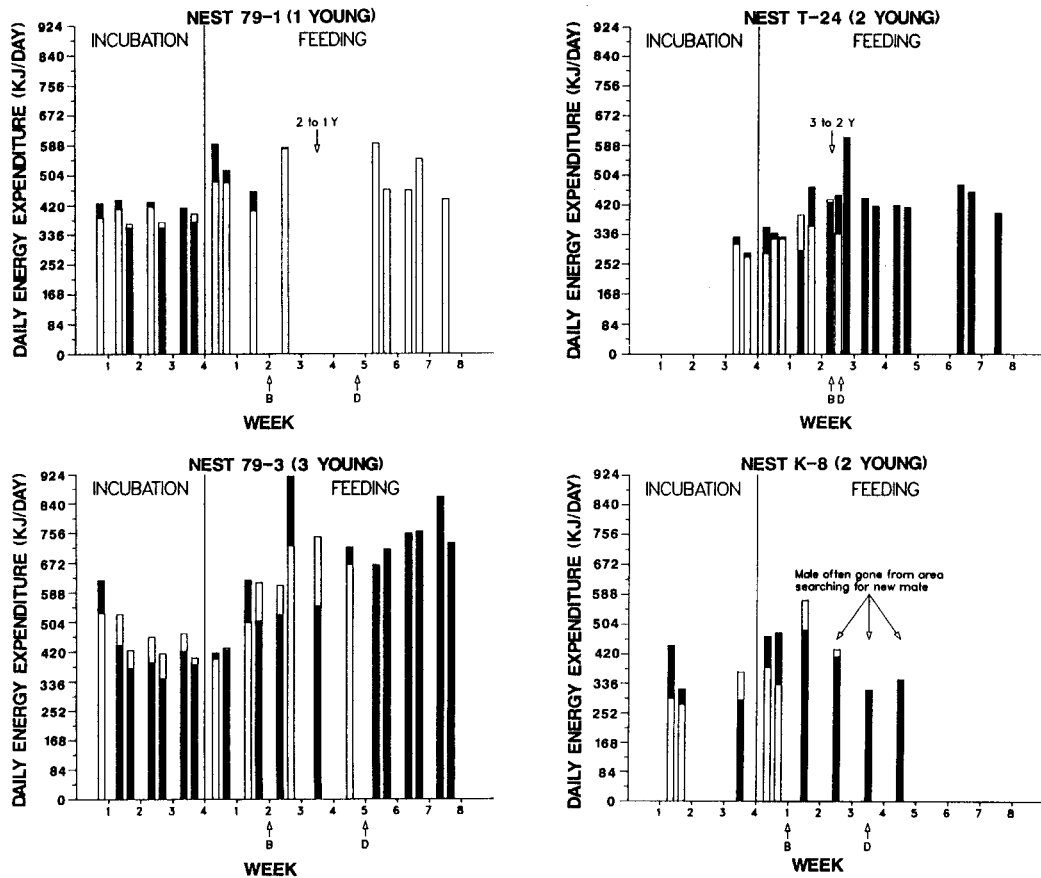
Figure 4. Daily observations of energy expenditure for males (closed bars) and females (open bars) at four snail kite nests from incubation through the termination of parental care. The end of Brooding (B), the onset of Monoparental Care after mate desertion (D), and changes in the number of young (Y) are shown.

investing less in feeding and, to some extent, brooding, than their mates.

The frequency of chases and risk incurred showed no apparent differences between tenders and deserters, and between deserted and non-deserted nests (Table I, Fig. 1C). On average, males did more chasing and consequently had higher risk scores than females, but the variance was high. There was no difference in the average risk incurred in chases by males and females (paired t-test, $N = 12$, $P = 0.526$).

Nests were sorted into clusters based on similarities in the execution of parental duties as measured by all 17 correlates of parental effort (Table I). The results (Fig. 3) suggest that nests associated most strongly with other nests that had a similar pattern of mate desertion. Three of four nests deserted by

males were clustered closely together in one group. However, one male-deserted nest (302) did not cluster with the others, but did with two non-deserted nests. This male deserted later in the nesting cycle than any of the other deserters (53 days after hatching versus an overall mean of 29 days; Beissinger & Snyder 1987). Apparently, parental care at this male-deserted nest resembled that of non-deserted nests more than other male-deserted nests.

If the relative amount of effort expended by a kite parent at a nest is important in determining which mate deserts, then how does the willingness of a parent to invest in one parental activity relate to its participation in future activities? This is a crude attempt to determine whether past expenditure of parental effort affects future expenditure of

Table III. Daily energy expenditure (DEE) for each parental care period during the nesting cycle

| Nest† | Sex‡ | $\bar{X} \pm$ SEM for DEE (kJ/day) during: | | | | |
		Incubation	Brooding	Post-brooding	Desertion	Between-period P
K-8 (2)	Male (T)	358 ± 47	473 ± 5	439 ± 42	NE§	0·100
	Female (D)	312 ± 28^a	355 ± 25^{ab}	500 ± 69^b	—	0·067
T-24 (2)*	Male (T)	306 ± 23^a	368 ± 27^{ab}	446^{abc}	453 ± 24^c	0·040
	Female (D)	289 ± 19	351 ± 22	336	—	0·390
79-1 (1)*	Male (D)	397 ± 13	522 ± 38^a	579^a	—	0·032
	Female (T)	398 ± 8	457 ± 26^a	577^b	500 ± 30^{ab}	0·003
79-3 (3)	Male (T)	424 ± 35^a	492 ± 48^a	675 ± 91^b	744 ± 27^b	0·001
	Female (D)	461 ± 19^a	486 ± 48^a	683 ± 30	—	0·001

For each individual, periods with the same letters are not significantly different from each other (Fisher's least significant difference test) if the one-way ANOVA *P*-value is significant.
† Brood size at desertion in parentheses. An asterisk indicates reduction of one young previous to desertion.
‡ Deserter (D) or tender (T).
§ Not estimated because male was lost too often.

parental effort (the Concorde fallacy, Dawkins & Carlisle 1976). Participation by snail kite mates in parental care behaviour was only weakly predictive of participation in future parental behaviour (Table II). Of the four major behaviours (incubating, brooding, feeding and chasing), there were only a few significant relationships between expended efforts and future efforts: (1) males that incubated more often and for longer than their mates also brooded more often and for longer; (2) males that incubated more often and for longer incurred higher average risks in chases than their mates; and (3) males that incubated for longer bouts were less involved in feeding nestlings during Brooding. Significant correlations did not occur between the amount of participation by a parent in feeding, the key correlate relating to desertion, and its participation in incubation, brooding, or chasing.

Significant correlations, mostly negative, were found for behaviours which do not occur independently, since performing one behaviour usually excluded the participant from performing another behaviour simultaneously (Table II). These were: (1) males that brooded more often increased their contributions to feeding during Post-brooding, when they were freed from nest attendance; and (2) during Brooding, males that fed nestlings more often incurred lower average risks than males that

provided fewer snails, perhaps because a male that is brooding is in a position to defend the nest more often than is a male that is foraging. Significant correlations were also found among measures that are not independent of each other, such as the relative percentage of brooding by males and the length of their brooding bouts. Finally, a last set of significant correlations occurs between incubation and brooding behaviour, and measures of parental neglect, such as the percentage of time that eggs or young were left uncovered during Incubation or Brooding.

Patterns of Energy Investment Versus Mate Desertion

Daily energy expenditures for males and females at four nests are shown in Fig. 4. No significant differences in average daily energy expenditure between deserters and tenders were noted during the entire biparental period at any nest (paired *t*-test, $P > 0.10$), in part because of the shifting of parental roles from one sex to the other that occurred throughout the nest cycle and the associated changes in metabolic costs of these activities. For instance, on a given day, the parent that incubated more often had consistently lower energy expenditures (sign test, $N = 18$ days, $P < 0.01$). Conversely, the parent that fed the
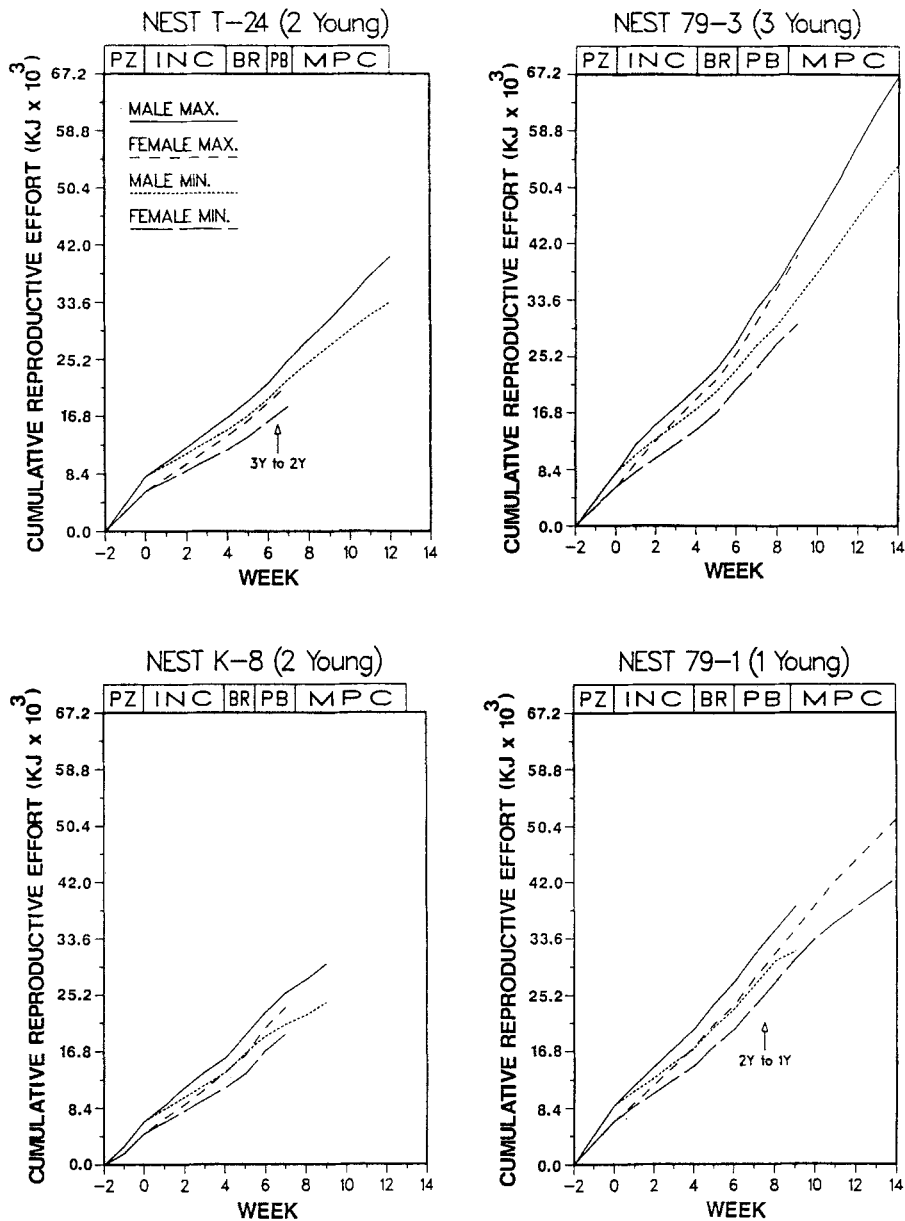
Figure 5. Cumulative energy investment as a profile of reproductive effort for male and female snail kites at four nests. Minimum (min.) and maximum (max.) estimates of reproductive effort (see Methods) are shown for each parent. Above the cumulative function, the duration of nesting cycle periods (PZ: Prezygotic; INC: Incubation; BR: Brooding; PB: Post-brooding; MPC: Monoparental Care) is shown. The number of young successfully fledged appears next to the nest number. Changes in brood size (Y) are indicated.

nestlings more often had a higher daily energy expenditure on that day (sign test, $N = 22$ days, $P < 0.05$).

A three-way ANOVA using repeated measures of daily energy expenditure (Table III) found significant differences among nests ($P = 0.001$) and

throughout the nesting cycle at a nest ($P=0.001$), and slighter differences ($P=0.058$) between males and females. When a factor for deserter type (male versus female) was used in the ANOVA model instead of sex, the difference in daily energy expenditure between deserters and tenders was not significant ($P=0.176$). No significant interaction terms were noted in either model. This analysis indicates that the energy cost of parental care increases throughout the nesting cycle and can vary from nest to nest, probably partly as a function of local snail densities and brood size.

The shapes of the curves of cumulative reproductive effort for snail kites (Fig. 5) were similar for all nests, but were quite different from Trivers' (1972: page 147) hypothetical curves. Investment accrued at a slightly higher rate during the Prezygotic period (Beissinger 1987), slowed during Incubation, and generally increased through Brooding and Post-brooding. After mate desertion, the slope of the tender's curve usually increased again and never slowed until parental care was nearly terminated. For the three nests where females deserted, the females had consistently lower values of cumulative energy expended until the point of mate desertion. But this was not true for the nest deserted by male 79-1. Even if the Prezygotic estimate of reproductive effort (which was higher for males than females, Beissinger 1987) was excluded from nest 79-1, cumulative investment was higher for the deserter at this nest.

The relative difference in reproductive effort between members of a pair was not as large as might have been expected. At desertion, deserters had invested 46.1%, 49.4% and 53.9% of the total RE_{max} invested to that pont (no values for K-8 due to incomplete data; Fig. 4). Differences in energy investment between mates at a nest were 1063, 3659 and 5581 kJ. Such differences are not trivial, representing approximately 3–15.5 days of daily energy expenditure for non-breeding kites (using Beissinger's 1983 estimate from South American snail kites).

An association in the timing of mate desertion and the cumulative expenditure of reproductive effort was noted at the three nests where reproductive effort could be measured until the young were independent (K-8 excluded). Mate desertion occurred when 75–79% of the total RE_{max} (76–81% of RE_{min}) for the bout had been invested, even

though desertion was nearly 2 weeks earlier at nest T-24 than at the other two nests, and brood size varied from one to three.

DISCUSSION

Mate Desertion and Reproductive Effort

The data on desertion in snail kites lend partial support to Trivers' (1972) prediction that the individual deserting should be the one that has invested less than its mate in a reproductive bout. Analysis of correlates of parental effort at 13 nests where mate desertion occurred indicated that only provisioning of young, the most energy-intensive parental activity, differed significantly between nest tenders and deserters, and was a good predictor of which sex would desert (Table I, Fig. 1). Decreased feeding by deserters was established within the first 2 weeks after hatching (Fig. 2). There was no difference in the participation by deserters or tenders in incubating, brooding, or nest-defence behaviour (Table I). Of the four nests where time–energy budgets were determined, females invested less reproductive effort than males in the three cases where the female deserted (Fig. 5). But in the case where the male deserted (79-1), the male had invested more than his mate, and the difference in reproductive effort between mates was larger at this nest than at any of the others.

Variability among snail kite pairs was high in the apportionment of parental care duties between the sexes. As a result, males had sometimes invested more, and sometimes less, reproductive effort than females at the moment of desertion. Variation in male and female contribution of reproductive effort may be a characteristic of ambisexual mate desertion systems (Beissinger 1987) and of conflict between mates (Hand 1985).

The decision to desert should be based on the costs and benefits, in terms of present and future fitness, of deserting to the deserter (Boucher 1977; Maynard Smith 1977; Alexander & Borgia 1979). Differences in reproductive effort may have predicted which snail kite mate deserted because it is related to both the costs and benefits of reproduction. Reproductive effort represents the cost of the present reproductive bout. Decreased reproductive success, the other possible cost to a deserter, rarely happens in kites because desertion usually occurs when the probability of nest failure is low, and

tenders nearly always successfully rear the young alone (Beissinger & Snyder 1987).

In addition to being an index of the cost of reproduction, reproductive effort is also an indicator of several factors that reflect the benefits of desertion. First, the cumulative total of reproductive effort expended is an index of the accrued benefits of a reproductive bout (in terms of how close the offspring are to independence). Second, reproductive effort expended in a bout may be an indicator of reproductive effort to be expended in future bouts. Within a reproductive bout, past effort by kites was weakly predictive of future effort (Table II). However, I have no long-term data on individuals from bout to bout, to test this prediction. Finally, the opportunity for multiple brooding, the third potential benefit of deserting, depends upon the availability of mates (i.e. the operational sex ratio), and whether environmental conditions and seasonality will permit another nesting attempt. Reproductive effort is probably a poor indicator of the opportunity to re-mate. However, individuals may adjust their reproductive efforts in response to perceived future opportunities for re-mating by assuming fewer parental responsibilities.

Thus, reproductive effort may have been related to which snail kite parent deserted because it is a good indicator of several aspects of the costs and benefits of desertion.

Other Factors Affecting the Costs/Benefits of Desertion in Kites

The opportunity to re-mate directly affects the benefits of desertion and sometimes appeared to be an important factor influencing which snail kite parent deserted. For instance, in 1982, more females deserted in one of my study areas and this may have been a response to the presence of several unmated males (Beissinger & Snyder 1987). At other nests, opportunities to re-mate appeared to be plentiful for both sexes, as many unpaired kites were present. However, the local availability of mates may not limit re-mating opportunities, since kites have moved as far as 160 km between successive nesting attempts within a season (Beissinger & Snyder 1987). Unfortunately, it is difficult to quantify the opportunity to re-mate because the operational sex ratio in snail kites cannot be determined.

The age of parents may affect mate desertion behaviour in two ways. First, nesting success may increase with experience (e.g. Coulson 1966; Wooler & Coulson 1977), so that experienced parents may be more capable of tending their young alone. Older individuals may also be more experienced at recognizing the best and earliest time to desert. Second, the costs of reproductive effort in a bout must be evaluated relative to each individual's reproductive value (Fisher 1930) and the amount of lifetime reproductive effort already expended (Williams 1966; Schaeffer 1974; Goodman 1979; Pugesek 1981). Deserting may be more important to older than younger individuals because older parents will have less remaining lifetime opportunities and residual effort to expend for future reproduction. The effects of age on desertion in snail kites was not determined.

Low confidence in paternity or maternity increases the likelihood of deserting or investing less reproductive effort (Alexander & Borgia 1979). Confidence of maternity is probably high in kites, as females remained close to the nest throughout most of the Prezygotic period, clutch size varied little, and dump nests were not observed (Beissinger 1986, 1987). Confidence in paternity should generally be high (Beissinger 1987) except when males choose to pair and mate rapidly with females. Such was the case at nest K-8, where the female had copulated frequently with another male less than a week before laying at her nest with male K-8. Despite a probably low confidence in paternity, this male was a tender; it appeared that he was ready to desert, since he was feeding the young less frequently and trying to provision a new mate at the same time, but returned to caring exclusively for the young after his mate deserted and immediately re-nested.

Reproductive Effort, Timing and Mate Desertion

Mate desertion in snail kites occurs after 75% of the total reproductive effort and time invested in a bout has elapsed, relatively late in the reproductive bout compared with other animals (Kleiman 1977; Ridley 1978; Perrone & Zaret 1979; Wells 1981; Oring 1982) and after the probability of nest failure is low (Beissinger & Snyder 1987). Because 68% of kite nests in Florida fail (Beissinger 1986), the chances are small that a tender could attain the same reproductive success (benefit) in a future bout. Tenders deserting their broods and starting over with new mates, in hopes of being deserters,

would lose the benefits accrued from all reproductive effort already invested, and are not likely to be favoured by selection. Therefore, the only viable option for a kite parent after being deserted is to continue caring for the young.

Thus, it seems that either parent should be tempted to desert, whether or not it had invested more reproductive effort than its mate, and mates may be in conflict over which one will desert. This conflict should escalate as the time of desertion nears. Perhaps both mates do attempt to desert. The high variation in the daily apportionment of reproductive effort between mates (Figs 1 and 4) could partly arise from this conflict (Hand 1985). The behaviour by kites immediately preceding desertion is hard to interpret and the actual act of deserting is difficult to observe.

Despite the high success of tenders in rearing the young alone (Beissinger & Snyder 1987), there is some risk of decreased reproductive success associated with deserting a mate and young. A deserter must be certan that its mate (1) has not already deserted and (2) is capable of caring for the young until the age of independence without losing any offspring. Deserters must also assess highly unpredictable Everglades water levels (Beissinger 1986), which strongly affect nest success and snail populations, to be certain that their continued effort is not needed to avoid losing young. During Post-brooding, mates begin to behave independently of each other for the first time since pairing, hunting for snails and delivering them to the nestlings. Because behaving independently decreases the amount of interaction between mates, the probability of detecting that a mate has deserted decreases. To be certain that a mate is capable of caring for the young alone and has not already deserted, potential deserters might be expected to decrease reproductive effort and test their mates. This process may start shortly after hatching when future deserters began to contribute less reproductive effort than their mates (Table I and Fig. 2). Individuals that hesitate too long to desert, because they are not confident of their mate's ability to be a successful parent alone, are likely to be deserted themselves. Since differences in reproductive effort between tenders and deserters may partly reflect the process of mate assessment that precedes desertion, at most nests it is unlikely that desertion would occur often, irrespective of previous expenditures of reproductive effort.

In conclusion, relative differences in reproductive effort or its correlates often, but not always, predicted which snail kite parent deserted its mate. This result was fairly consistent with Trivers' (1972) hypothesis, but may not necessarily support his explanation of causation. Reproductive effort may have been predictive because it is a good indicator of the costs and benefits of desertion. Because snail kites desert their mates late in a nesting cycle, relative differences in reproductive effort may be less important in determining which parent should desert than other factors, such as which mate recognizes the earliest possible moment to leave or has the best opportunity to re-mate. To paraphrase Trivers (1972, page 144), sexual selection (mate desertion and the mating system) is controlled by both the relative differences in reproductive effort between mates and a force that affects that pattern. In snail kites, it is not clear whether differences in reproductive effort act solely as a causal factor in the desertion decision or whether some of the differences are a result of parents adjusting their expenditure of reproductive effort in response to other factors.

ACKNOWLEDGMENTS

REFERENCES

Alexander, R. D. & Borgia, G. 1979. On the origin and basis of the male–female phenomenon. In: *Sexual Selection and Reproductive Competition in Insects* (Ed. by M. S. Blum & N. A. Blum), pp. 417–440. New York: Academic Press.

Anderson, M. G. 1984. Parental investment and pair-bond behavior among canvasback ducks (*Aytha valisneria*, Anatidae). *Behav. Ecol. Sociobiol.*, **15**, 81–90.

Andersson, M., Wiklund, C. G. & Rundgren, H. 1980. Parental defence of offspring: a model and an example. *Anim. Behav.*, **28**, 536–542.

Aschoff, J. & Pohl, H. 1970. Rhythmic variations in energy metabolism. *Fed. Proc., Fed. Am. Soc. exp. Biol.*, **29**, 1541–1552.

Beissinger, S. R. 1983. Hunting behavior, prey selection and energetics of snail kites in Guyana: consumer choice by a specialist. *Auk*, **100**, 84–92.

Beissinger, S. R. 1984. Mate desertion and reproductive effort in the snail kite. Ph.D. thesis, University of Michigan, Ann Arbor.

Beissinger, S. R. 1986. Demography, environmental uncertainty, and the evolution of mate desertion in the snail kite. *Ecology*, **68**, 1445–1459.

Beissinger, S. R. 1987. Anisogamy overcome: female strategies in snail kites. *Am. Nat.*, **129**, 486–500.

Beissinger, S. R. In press. The snail kite. In: *Handbook of North American Birds, Vol. IV* (Ed. by R. S. Palmer). New Haven: Yale University Press.

Beissinger, S. R. & Snyder, N. F. R. 1987. Mate desertion in the snail kite. *Anim. Behav.*, **35**, 477–487.

Beissinger, S. R. & Takekawa, J. E. 1983. Habitat use by and dispersal of snail kites in Florida during drought conditions. *Fla Field Nat.*, **11**, 89–106.

Boucher, D. H. 1977. On wasting parental investment. *Am. Nat.*, **111**, 786–788.

Coleman, R. M., Cross, M. R. & Sargent, R. M. 1985. Parental investment decision rules: a test in bluegill sunfish. *Behav. Ecol. Sociobiol.*, **18**, 59–66.

Congdon, J. D., Whitfield Gibbons, J. & Greene, J. L. 1983. Parental investment in the chicken turtle (*Deirochelys reticularia*). *Ecology*, **64**, 419–425.

Coulson, J. C. 1966. The influence of the pair-bond and age on the breeding biology of the kittiwake gull (*Rissa tridactyla*). *J. Anim. Ecol.*, **35**, 269–279.

Dawkins, R. & Brockman, H. J. 1980. Do digger wasps commit the Concorde fallacy? *Anim. Behav.*, **28**, 892–896.

Dawkins, R. & Carlisle, T. R. 1976. Parental investment, mate desertion and a fallacy. *Nature, Lond.*, **262**, 131–132.

Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. New York: Dover.

Gessaman, J. A. & Findell, P. R. 1979. Energy cost of incubation in the American kestrel. *Comp. Biochem. Physiol. A*, **63**, 57–62.

Goodman, D. 1979. Regulating reproductive effort in a changing environment. *Am. Nat.*, **113**, 735–748.

Grafen, A. & Sibly, R. 1978. A model of mate desertion. *Anim. Behav.*, **26**, 645–652.

Grant, G. R. 1984. Energy cost of incubation to the parent seabird. In: *Seabird Energetics* (Ed. by G. C. Whitlow & H. Rahn), pp. 59–71. New York: Plenum Press.

Hand, J. L. 1985. Egalitarian resolution of social conflicts: a study of pair-bonded gulls in nest duty and feeding contexts. *Z. Tierpyschol.*, **70**, 123–147.

Hirschfield, M. F. & Tinkle, D. W. 1975. Natural selection and the evolution of reproductive effort. *Proc. natn. Acad. Sci. U.S.A.*, **72**, 2227–2231.

Howell, A. H. 1932. *Florida Bird Life*. New York: Coward-McCann.

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.

Kendeigh, S. C., Dol'nik, V. R. & Gavrilov, V. M. 1977. Avian energetics. In: *Granivorous Birds in Ecosystems* (Ed. by J. Pinowski & S. C. Kendeigh), pp. 127–204. New York: Cambridge Press.

Kleiman, D. G. 1977. Monogamy in mammals. *Q. Rev. Biol.*, **52**, 39–69.

Koplin, J. R., Collopy, M. W., Bammann, A. R. & Levenson, H. 1980. Energetics of two wintering raptors. *Auk*, **97**, 795–806.

Low, B. S. 1978. Environmental uncertainty and the parental strategies of marsupials and placentals. *Am. Nat.*, **112**, 197–213.

Maynard Smith, J. 1977. Parental investment: a prospective analysis. *Anim. Behav.*, **25**, 1–9.

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. London: Cambridge University Press.

Mugaas, J. N. & King, J. R. 1981. The annual variation in daily energy expenditure of the black-billed magpie: a study of thermal and behavioral energetics. *Stud. Avian Biol.*, **5**, 1–78.

Oring, L. W. 1982. Avian mating systems. In: *Avian Biology. Vol. VI* (Ed. by D. S. Farner, J. R. King & K. C. Parkes), pp. 1–92. New York: Academic Press.

Patterson, C. B., Erckmann, W. J. & Orians, G. H. 1980. An experimental study of parental investment and polygyny in male blackbirds. *Am. Nat.*, **116**, 757–769.

Perrone, M., Jr & Zaret, T. M. 1979. Parental care patterns of fishes. *Am. Nat.*, **113**, 351–361.

Pugesek, B. H. 1981. Increased reproductive effort with age in the California gull (*Larus californicus*). *Science, N.Y.*, **212**, 822–823.

Ridley, M. W. 1978. Paternal care. *Anim. Behav.*, **26**, 904–932.

Robertson, R. J. & Biermann, G. C. 1979. Parental investment strategies determined by expected benefits. *Z. Tierpsychol.*, **50**, 124–128.

Røskaft, E. 1983. Sex-role partitioning and parental care by the rook *Corvus frugilegus*. *Ornis Scand.*, **14**, 180–187.

Schaeffer, W. W. 1974. Selection for optimal life histories: the effects of age structure. *Ecology*, **55**, 291–303.

Snyder, N. F. R. & Snyder, H. A. 1969. A comparative study of mollusc predation by limpkins, Everglade kites and boat-tailed grackles. *Living Bird*, **8**, 177–233.

Snyder, N. F. R. & Wiley, J. W. 1976. Sexual size dimorphism in hawks and owls of North America. *Ornithol. Monogr.*, **20**, 1–96.

Sykes, P. W., Jr & Kale, H. W., II. 1974. Everglades kites feed on nonsnail prey. *Auk*, **91**, 818–820.

Tinkle, D. W. 1969. The concept of reproductive effort and its relation to the evolution of life histories of lizards. *Am. Nat.*, **103**, 501–516.

Tinkle, D. W. & Hadley, N. F. 1975. Lizard reproductive effort: caloric estimates and comments on its evolution. *Ecology*, **56**, 427–434.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.

Vleck, C. M. 1981. Energetic cost of incubation in the zebra finch. *Condor*, **83**, 229–237.

Walsberg, G. E. 1983. Avian ecological energetics. In: *Avian Biology. Vol. VII* (Ed. by D. S. Farner, J. R. King & K. C. Parkes), pp. 161–220. New York: Academic Press.

Walsberg, G. E. & King, J. R. 1978. The energetic consequences of incubation for two passerine species. *Auk*, **95**, 644–655.

Weatherhead, P. J. 1979. Do savannah sparrows commit the Concorde fallacy? *Behav. Ecol. Sociobiol.*, **5**, 373–381.

Weathers, W. W., Buttemer, W. A., Hayworth, A. M. & Nagy, K. A. 1984. An evaluation of time-budget estimates of daily energy expenditure in birds. *Auk*, **101**, 459–472.

Wells, K. D. 1981. Parental behavior of male and female frogs. In: *Natural Selection and Social Behavior* (Ed. by R. D. Alexander & D. W. Tinkle), pp. 184–197. New York: Chiron Press.

Williams, G. C. 1966. *Adaptation and Natural Selection*. Princeton: Princeton University Press.

Williams, J. B. & Nagy, K. A. 1984. Daily energy expenditure of savannah sparrows: comparison of time–energy budget and doubly-labeled water estimates. *Auk*, **101**, 221–229.

Wooler, R. D. & Coulson, J. C. 1977. Factors affecting the age of first breeding of the kittiwake *Rissa tridactyla. Ibis*, **119**, 339–349.