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ANISOGAMY OVERCOME: FEMALE STRATEGIES IN SNAIL KITES

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Reproductive effort (RE) is the total expenditure of risk and energy incurred by a parent in reproduction (Williams 1966; Gadgil and Bossert 1970; Hirschfield and Tinkle 1975). It may be divided into mating effort (ME), used to secure copulations, or parental effort (PE), used to produce offspring (Low 1978; Alexander and Borgia 1979). For instance, at the start of a reproductive bout, females may invest heavily in gamete production (PE), whereas males may invest heavily by competing with other males to secure matings (ME). Many authors (e.g., Trivers 1972, 1985; Wilson 1975; Dawkins 1976) have suggested that, because of anisogamy (in which females produce a few energy-rich eggs and males produce many energetically cheaper sperm), females usually invest more RE than do males by the time of fertilization.

Trivers (1972) formalized these ideas into a theory of parental investment, which recognized that mating systems may be a function of the relative disparity in RE invested by the sexes. Trivers' hypothesis predicts that if RE by the sexes in a given reproductive bout is unequal, the parent that invests less than its mate should be more tempted to desert. Dawkins and Carlisle (1976) and Boucher (1977) pointed out that 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. Factors affecting the costs and benefits of desertion include the potential for decreased or increased reproductive success by deserting, confidence in paternity or maternity, and age as it relates to reproductive value (Fisher 1930) and experience (Dawkins and Carlisle 1976; Boucher 1977; Alexander and Borgia 1979). Anisogamy, however, is often viewed as a major factor influencing parental investment patterns and the resulting mating systems, since it implies unequal reproductive investment and opportunity costs (Wilson 1975; Wittenberger 1981; Daly and Wilson 1983).

To demonstrate clearly that unequal investment by the sexes occurs before

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fertilization, some measure of RE must be quantified for each sex throughout the prezygotic period. Energy may be useful in this capacity because time-energy budgets can be coupled with laboratory or literature estimates of the energetic cost to females of egg laying and to males of sperm production in order to approximate reproductive-investment patterns (Hirschfield and Tinkle 1975; Walsberg 1983). Assessing risks associated with reproduction is more difficult but may be accomplished by monitoring the most risky behaviors, particularly, defending the nest from predators or conspecifics (Andersson et al. 1980).

The snail kite (*Rostrhamus sociabilis plumbeus* Ridgeway), a Neotropical hawk that nests in loose colonies and normally lays two or three asynchronously hatching eggs over a 2–7-day interval (Nicholson 1926; Bent 1937; Chandler and Anderson 1974; Beissinger 1986), is an excellent organism for examining patterns of reproductive investment. Kites usually inhabit open marshes and are relatively large, permitting the observation of their daily activities required for the construction of time-energy budgets. This raptor feeds almost exclusively on freshwater *Pomacea* snails (Howell 1932; Haverschmidt 1962; Snyder and Snyder 1969; Sykes and Kale 1974; Beissinger 1983; Snyder and Kale 1983), which facilitates analyses of energy and nutrient ingestion. Finally, in Florida this kite has an unusual mating system: if snails are abundant, either parent may desert its mate near the time of fledging (3–5 wk before the termination of parental care), sometimes taking a new mate and renesting (Beissinger and Snyder 1987). Females and males desert their mates at similar frequencies, and offspring mortality rarely occurs after desertion. Because deserters usually appear to invest less RE than their mates before desertion (Beissinger 1984), the patterns of RE investments before egg laying may have significant effects on future reproduction.

During a 5-yr study of mate desertion and RE in the endangered Florida population (Beissinger 1984), I assessed RE by male and female snail kites throughout pair formation and egg laying (the prezygotic period), using time-activity budgets and reproductive bioenergetics.

METHODS

Field studies were conducted from 1979 to 1983 throughout southern Florida wetlands in Broward, Collier, Dade, Glades, Hendry, Okeechobee, and Osceola counties. (For specific dates of the study, location of study areas, and description of environmental conditions, see Beissinger and Takekawa 1983; Sykes 1983; Beissinger 1984, 1986; Beissinger and Snyder 1987.)

The diurnal behavior of nesting snail kites was observed with binoculars or spotting scopes for 202 h during the prezygotic period, at distances of 75–200 m from the nest site, using a canoe, airboat, tree blind, or observation tower. Time-activity budgets were constructed from direct observations at seven nests. Behavior of the parents was observed almost continuously for 3-h to 10-h sample periods and timed to the nearest second using a stopwatch or digital wristwatch. Categories of behavior recorded are defined in Beissinger (1983, 1984; Beissinger and Snyder 1987). Daily energy expenditure (DEE) was calculated from time-activity budgets using an energetics model for wintering raptors (Koplin et al. 1980)

adapted for the breeding season by substituting summer (breeding) estimates of existence metabolism (Kendeigh et al. 1977). A detailed account of this energetics model is developed elsewhere (Beissinger 1984, MS). Tests of similar existence-metabolism and DEE-based energetics models have shown that they accurately approximate energy expenditures in field situations (Koplin et al. 1980; Williams and Nagy 1984; Weathers et al. 1984).

RE correlates were measured for each parent at the seven time-budget nests and at nine additional nests. These correlates included the number of sticks contributed to the nest, the number of aggressive chases of potential predators or conspecifics, and the number of snails delivered by the male to his mate.

Using standard methods (Horowitz 1970), W. G. Bergen of Michigan State University conducted proximate analyses on five unhatched kite eggs that were salvaged and on six *Pomacea paludosa* snails. Kite eggs and snail bodies were removed from the shell and dried at 60°C for 36 h. Protein, lipid, ash, and caloric content were determined for both eggs and snails. Results were used to estimate the caloric cost of egg production for female kites (cf. Walsberg 1983).

Cumulative curves of RE investment were generated for each sex. For the prezygotic period, two models were developed to illustrate the effect of a rapid or slow period of pair formation on the patterns of investment. In the rapid model, RE for both members of the pair begins immediately on day 1, egg laying begins on day 7, and the clutch is complete on day 11. This model represents a minimum estimate of male RE based on field observations of the minimum known period of pair formation. In the slow model, 4 days of male ME are required to acquire a mate, female RE begins only after pairing is established on day 5, egg laying begins 10 days later, and the clutch is completed 5 days later. This model is closer to the average estimate of male RE using average time intervals for pair-formation activities from several nests, although the 4-day estimate for a male to secure a mate may be a conservative approximation.

Estimates for parameters of the prezygotic RE model were derived as follows. An overall mean for DEE was calculated for males and for females using the data from seven pairs observed during the prezygotic period. Only one day of observation of male DEE before pairing (162 kcal per day) was obtained for this period. Female RE included both the costs of clutch production, allocated throughout the whole prezygotic period, and an estimate of female DEE. The cost of gametogenesis was assumed to be negligible for males (Ricklefs 1974; Walsberg 1983). Using the 75% confidence interval or error bound of DEE calculated from Chebyshev's inequality (Steel and Torrie 1960), maximum and minimum daily limits of effort were calculated. These limits encompass 95% of the values for mean RE of males and females assuming a normal distribution, and at least 75% for other distributions. Minimum and maximum daily RE estimates were cumulated in a linear fashion for the number of days in each model.

Statistical analyses were conducted on the University of Michigan Amdahl 470v/8 computer. Means are reported with standard deviations (SD) and sample sizes (N). 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. Nonparametric statistics were used when these assumptions were violated.

Large differences in prezygotic investment between the sexes were found (fig. 1). Males spent significantly more time foraging than females (28% vs. 7%; Wilcoxon signed-ranks test, $P < 0.01$), and they spent more time feeding their mates than these females spent foraging for themselves (Wilcoxon signed-ranks test, $P < 0.01$). As a result of these differences in foraging behavior, males provided 56%–100% ($\bar{x} = 83\%$) of the snails ingested by females during the observation periods (fig. 1). Males fed females at a rate of 1.31 ± 0.61 snails per h ($N = 16$ nests), whereas females fed themselves 0.23 ± 0.23 snails per h ($N = 7$ nests). Females that laid clutches of three tended to receive more food from courting males (1.24 ± 0.11 snails per h, $N = 4$) than females that laid clutches of two (0.86 ± 0.13 snails per h, $N = 4$), but this difference was not statistically significant ($U_{4,4} = 14$, $P = 0.10$). Besides supplying most of the females' food, males contributed more to nest building, supplying 80.5% ± 20.1% of the sticks (sign test, $N = 16$ nests, $P < 0.002$), and to excluding potential predators and other kites (males chased three times as often as females; sign test, $N = 9$ nests, $P < 0.02$).

The vast differences in male and female behavior are amplified by differences in energetic expenditures (fig. 2). Male DEE averaged 134.2 ± 17.6 kcal per day, nearly twice that of females (76.3 ± 8.7 kcal per day; paired t-test, $N = 7$, $P < 0.001$). DEE by females during the prezygotic period was generally less than during incubation (86.9 ± 18.7 kcal per day, $N = 4$) and caring for the young (125.2 ± 34.9 kcal per day, $N = 4$); however, male prezygotic DEE was higher than male expenditures during incubation (88.7 ± 12.23 kcal per day, $N = 4$) but similar to DEE in caring for the young (127.8 ± 27.1 kcal per day, $N = 4$). Differences in prezygotic DEE values between males and females were a result of the high percentage of time that males spent in the energetically costly flight activities of various courtship behaviors. Unusually high DEE values at nest 3A-1 in 1982 resulted from low snail populations, an effect of the 1981–1982 drought (Beissinger and Takekawa 1983). Eggs were never laid at this nest, probably because the male was unable to provide the female with enough snails. Because of these unusually severe conditions, days when male 3A-1 had difficulty provisioning the female were excluded to avoid inflating estimates of male RE. The other high male DEE value occurred at nest 79-1 during a winter cold front, which sometimes can cause a sharp decline in foraging success (Carey 1985; Beissinger, Snyder, and G. A. Falxa, unpubl. data).

Models of cumulative energy investment (see Methods) as estimates of RE can be constructed by adding the costs of clutch production for the female (table 1) to estimates of female DEE (fig. 3). Both the male minimum-expenditure model (rapid pair formation) and the male average-expenditure model (slower pair formation) indicate that males invested more energy than females through the egg-laying period.

Female RE may be underestimated in the previous models if females must invest endogenous energy or dietary reserves in clutch production, as has been shown for waterfowl and geese that lay energy-rich eggs producing precocial

A. CHASES AND STICKS

	70(9)	4(5)	16(0)	16(2)	7(1)	9(0)	44(17)

%STICKS — 100, 80, 60, 40, 20, 0

% CHASES — 0, 20, 40, 60, 80, 100

NESTS   79-1   K-3   K-5   K-8   K-9   T-11   3A-1

B. SOURCE OF FEMALE'S FOOD

MALE/MALE+FEMALE — 100, 80, 60, 40, 20

C. PERCENT OF TIME SPENT FORAGING

% TIME FORAGING — 40, 30, 20, 10

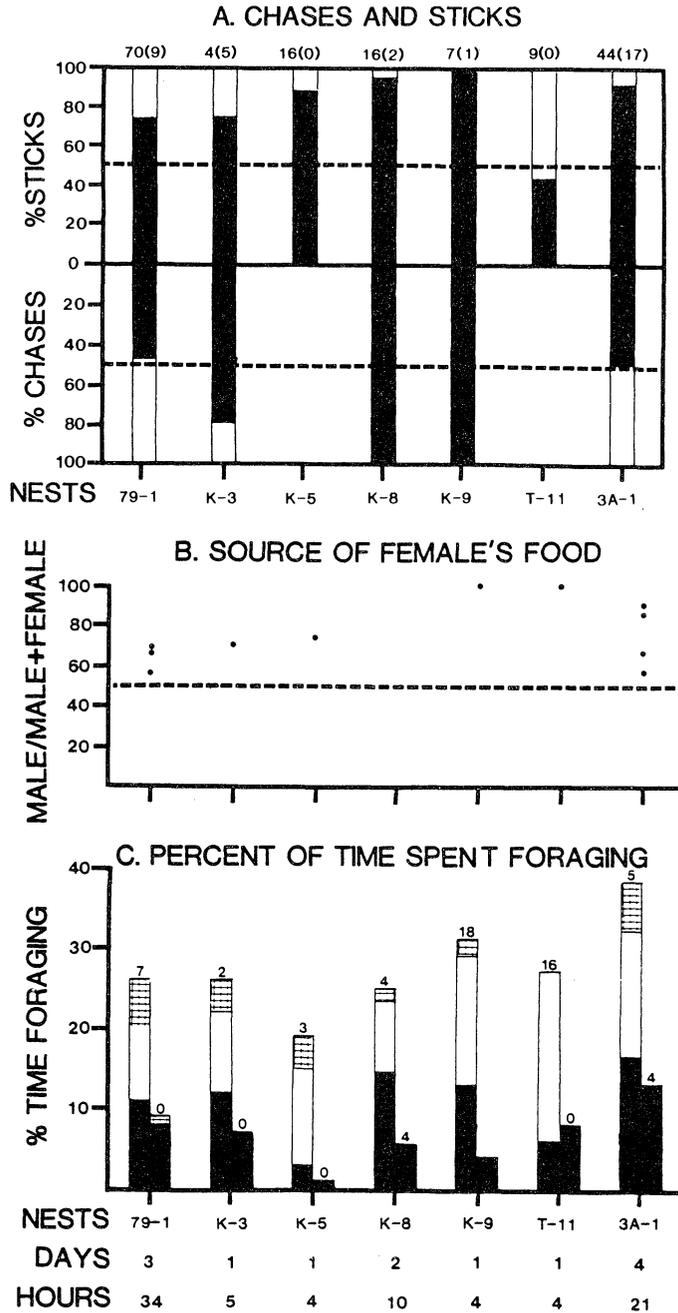| NESTS	79-1	K-3	K-5	K-8	K-9	T-11	3A-1
DAYS	3	1	1	2	1	1	4
HOURS	34	5	4	10	4	4	21

FIG. 1.—Prezygotic investment profiles for seven snail kite pairs. *A*, The number of sticks brought to the nest (and chases of other kites and potential predators) appear above each bar. *Solid bars*, male percentages of the total; *open bars*, female percentages. *B*: *solid circles* indicate the values of one observation period; *square*, two similar values from two observation periods. *C*, For each nest, bars indicating males are on the left, those indicating females on the right. The percent of time spent foraging by a kite: *solid bars*, for itself; *open bars*, for a mate; *striped bars*, unknown. The percent of time that a bird was lost from view appears above each bar.
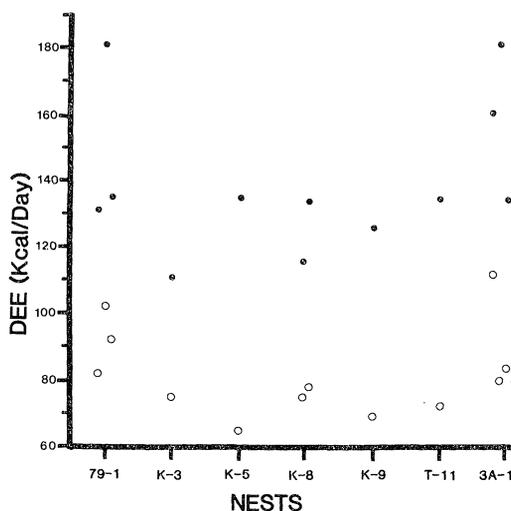
FIG. 2.—The daily energy expenditure (DEE) in kcal per day during the prezygotic period: *solid circles*, for males; *open circles*, for females. For nests with multiple observations, observation days of males and females are vertically aligned.

TABLE 1

SUMMARY OF THE CALORIC COSTS (kcal) TO FEMALE SNAIL KITES FOR THE PRODUCTION OF A THREE-EGG CLUTCH AND FOR BIOSYNTHESIS OF EGGS AND OVARY TISSUE

REPRODUCTIVE MATERIAL	SOURCE OF COST		
	Production	Biosynthesis	Total
Three-egg clutch	87.0*	26.0†	113.0
Oviduct	39.9‡	32.7§	72.6
TOTAL COST			185.6

* Caloric content of 1 egg = 29.0 kcal based on a mean dry weight of 4.38 ± 0.30 g at a caloric content of 6.62 ± 0.07 kcal per g (Beissinger 1984).

† Estimated at 77% net production efficiency (Brody 1945; Drobney 1980).

‡ Calculated from Walsberg (1983, p. 168).

§ Estimated at 55% net production efficiency (Drobney 1980).

young (Ankney 1977; Drobney 1980; Krapu 1981). Analysis of snail-ingestion rates (Beissinger 1984) indicate that, on the average, total energy intake by females (134.8 ± 50.3 kcal per day) is sufficient to fuel daily energy needs (98.2 ± 9.7 kcal per day) during the egg-laying period. Daily energy needs of females were estimated using 76.3 ± 8.7 kcal per day for DEE (fig. 2), an assimilation efficiency of 0.9 (Sarker and Naulleau 1981; Beissinger 1983), and a cost of clutch production of 13.3 kcal per day (table 1) throughout a 2-wk period of rapid follicle growth and egg laying (Walsberg 1983). The rate of energy ingested, however, showed a high degree of variation among females, indicating that in some instances females
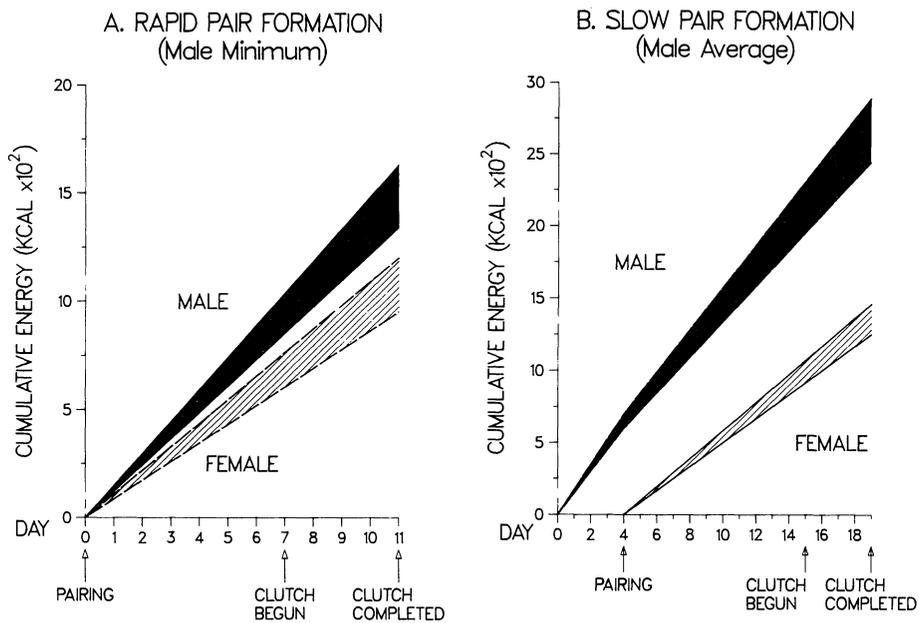
A. RAPID PAIR FORMATION
(Male Minimum)

B. SLOW PAIR FORMATION
(Male Average)

Fig. 3.—The cumulative energy invested by male and female snail kites during the prezy-gotic period: A, with rapid pair formation (male minimum model), in which males find and pair with females quickly and egg laying begins after 1 wk; B, with slower pair formation (male average model), in which males invest in displaying and nest building for 4 days before securing a female, and egg laying starts 10 days later. See the Methods section for model details.

might require reserves for egg production. Proximate analyses (table 2) indicate that although snails are a relatively rich source of protein, such that females are unlikely to require endogenous protein reserves, they are low in lipids, especially compared with the lipid content of a kite egg. Females would require 8.5 days of snail intake at a 70% net production efficiency (Brody 1945; Drobney 1980) to acquire enough lipids for a clutch, assuming that there is no intermediate metabolic conversion of protein to lipids. Since the normal period of ovary development and egg laying is 2 wk, it seems unlikely that lipid needs for egg production would necessitate use of endogenous reserves, thereby increasing female RE.

DISCUSSION

By the end of egg laying, male snail kites had consistently expended greater RE than females. The average energetic cost to males of gaining access to matings was much higher than the combined costs to females of egg production and daily activities (fig. 3). In addition, males were more active, hunting for snails and chasing predators or other males (fig. 1), whereas females remained perched near the relatively safe nest site; therefore, males were also likely to be taking greater risks than females.

TABLE 2

ANALYSIS OF LIPID AND PROTEIN IN SNAIL KITE
EGGS AND *Pomacea paludosa* SNAILS

Component	Present in Kite Eggs	Ingested in Snail Tissue
Per egg		
Lipid (%)	33.5 ± 1.0	3.1 ± 0.5
Protein (%)	44.4 ± 0.6	61.5 ± 5.2
Per clutch*		
Lipid (g)	4.4	0.7†
Protein (g)	5.8	14.5†

* Assuming average clutch size of three and dry egg weight of 4.38 g (Beissinger 1984).

† Expressed as grams per day ingested, assuming an average snail dry weight of 1.07 g and intake of 22 snails per day (Beissinger 1984).

Many authors have suggested that egg production is generally expensive and females are likely to have invested more than males at the moment of conception (e.g., Trivers 1972, 1985; Wilson 1975; Dawkins 1976). But others have predicted the opposite for species in which males must invest effort in finding and courting females (Low 1978; Ridley 1978; Alexander and Borgia 1979; Gladstone 1979; Walsberg 1983; Partridge and Halliday 1984). To my knowledge, this paper presents the first empirical evidence of higher male prezygotic investment, although other studies of monogamous birds have alluded to it (Montevecchi and Porter 1980; Burger 1981; Werschkul 1982). Males can make large investments before egg laying through the production of sperm in insects and fishes (e.g., Boggs and Gilbert 1979; Gwynne 1981; Dewsbury 1982; Nakatsuru and Kramer 1982), through the presentation of nuptial gifts in arthropods and birds (e.g., Royama 1966; Krebs 1970; Thornhill 1976, 1981; Nisbet 1973, 1977), and through mate guarding (e.g., Beecher and Beecher 1977; Birkhead 1979). But none of these researchers was able to demonstrate convincingly that males had invested more prezygotic RE than females because they lacked complete estimates of the costs of metabolic activity or reproductive efforts for both sexes.

Prezygotic RE of female snail kites is lower than that of males because females pursue a strategy, sometimes found in other bird species, of reducing energy demands during egg laying by decreasing locomotor activity (Walsberg 1983). Male activity during the same period is very high because of ME behaviors such as feeding his mate, building a nest, and excluding other males. By decreasing locomotor activity and depending on males to provide most of the energy required for egg production (fig. 1), females are able to withhold energy investment and avoid energy depletion during egg laying. More importantly, a female that withholds energy investments may be able to replace clutches soon after nest failure because a clutch is a relatively low energetic expense for a female assisted by a male, and because the female has not used her endogenous reserves. Increased iteroparity in female snail kites should be highly favored because, on the average,

68% of the nesting attempts are unsuccessful during the long breeding season (up to 10 mo) in Florida, partly as a result of the highly unpredictable fluctuations of Everglades water levels and, therefore, of the snail populations (Kushlan 1975; Beissinger 1986). Iteroparity is strongly favored in long-lived organisms when reproductive failure is due mostly to factors unaffected by the degree of parental care (Low 1976, 1978; Stearns 1976; Goodman 1979). This is the case for kites, whose nests often fail from structural collapse caused by poor substrates and/or high winds (Beissinger 1986). Selection for increased iteroparity, even at the expense of a modest decrease in clutch size, may also have led directly to mate-desertion behavior in snail kites since such desertion does not cause nesting failure (Beissinger 1986; Beissinger and Snyder 1987).

Courtship feeding by males allows females to withhold energy investments successfully and may be the key activity in pair formation in snail kites. Courtship feeding can be considered ME for males and PE for females (Alexander and Borgia 1979): males must invest ME in feeding females, which in turn use it for producing eggs. Snails from courtship feeding appear to be the primary source of energy for egg production (fig. 1), and females fed more often by their mates tended to lay larger clutches (e.g., Nisbet 1973). In addition to supplying energy for egg production, however, courtship feeding may play an important role in mate choice. Until they pair, females can be fed by more than one male during courtship. Thus, females may use snail-delivery rates to assess a male's genetic quality or his potential ability to give parental care. I observed two instances of pair bonds that appeared to dissolve when the males were unable to feed the females consistently during the prezygotic period. Females choosing males that are effective foragers may be able to desert their mates earlier to begin a new nesting cycle. However, males with superior foraging ability are also attractive to other females and may have good prospects for remating that could incline them to desert. Unfortunately, few data are available to examine the relationship between courtship-feeding rates and mate-desertion patterns. It is important to note that in some birds courtship feeding may also occur throughout the incubation period (Lack 1940; Royama 1966; Yamagishi and Saito 1985); however, male snail kites usually stopped feeding their mates immediately after egg laying had been completed, indicating an unwillingness to invest further in this costly activity.

A general model, derived from the preceding arguments (fig. 4), illustrates one way that selection could cause male RE to exceed female RE during the prezygotic period. Two key factors are involved in driving this hypothetical schema. First, in unpredictable environments, selection should act more strongly on the allocation of female RE than on that of male RE (Beissinger 1986). This occurs, as Low has suggested (1976, 1978), because iteroparous females may respond to environmental uncertainty in more ways (e.g., altering the timing of reproduction, clutch size, egg weight, clutch asynchrony, and the degree of multiple brooding) than males can (e.g., adjusting the timing of reproduction and possibly the degree of polygyny, but at best only influencing, not controlling, clutch size and egg weight). When reproductive failure is caused by factors unaffected by the degree of parental care in an unpredictable environment, females may be selected to minimize losses by cutting their costs in clutch production and becoming more

HIGHLY UNPREDICTABLE ENVIRONMENT

FEMALES SELECT MALES WHO COURTSHIP FEED

FEMALES INCREASE ITEROPARITY, DECREASE COSTS IN CLUTCH PRODUCTION

MALE INVESTMENT > FEMALE INVESTMENT

HIGH NEST FAILURE RATE

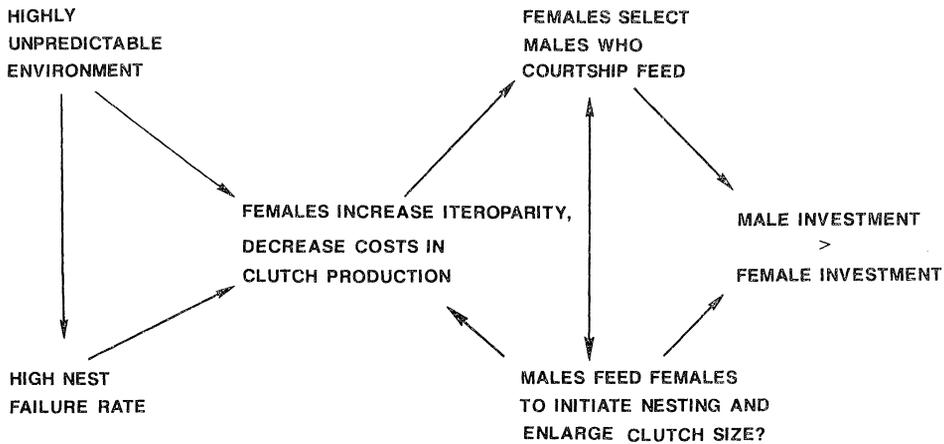MALES FEED FEMALES TO INITIATE NESTING AND ENLARGE CLUTCH SIZE?

FIG. 4.—One possible evolutionary pathway that would select for male RE to exceed female RE before egg laying. See text for details.

iteroparous because each breeding attempt may have an independent probability of being successful (Low 1976, 1978; Stearns 1976; Goodman 1979). Second, males may respond to females that decrease clutch size or hesitate to nest by trying to encourage nesting and to elevate clutch size through courtship feeding. Male behavior would then complement the action of selection on females, driving the system toward higher male RE and lower female RE through egg laying.

Two aspects of the behavior of female snail kites before egg laying appear unlikely to maximize reproductive success. First, females may not be maximizing their rate of egg production by being "waited on" by males if this results in a longer prezygotic period and a reduced number of clutches produced per year. For snail kites, however, the long breeding season probably offsets the costs to females of a lengthened prezygotic period because the prezygotic period is relatively short (only ⅙ of the total time required for one nesting cycle or 7% of the time potentially available for nesting), and delaying clutch production would not forfeit reproduction entirely. Females may even be able to determine the disparity of RE by controlling the length of the prezygotic period before egg laying begins (e.g., fig. 3). Early in the nesting season, prezygotic periods could be longer and females could afford to force males to invest more because time is less limited; later, females should proceed more quickly in order to have enough time to complete a reproductive bout successfully. Variability in the magnitude of differences in RE by males and females during the prezygotic period may be an important factor influencing which kite parent will desert its mate since deserters were usually, but not always, the parent that appeared to have invested less RE (Trivers 1972; Beissinger 1984, MS).

Second, if snails are abundant, females might maximize energy intake by hunting for themselves as well as by accepting food from males. Most females did use this strategy. Females that frequently foraged for themselves, however, probably forfeited some energy intake donated by males because males returning

to the nest area with snails and without encountering their mates often ate the mollusk themselves. Because females of some species may become heavier before egg laying, it is possible that they maximize energy assimilation at this time by avoiding the energetically costly maneuvers of flight and prey capture (Nisbet 1977).

One could argue that male snail kites make large initial investments of RE to increase confidence of paternity, by ensuring that mates never leave the nest area during egg laying (e.g., Power 1980). But confidence of paternity in snail kites is probably unrelated to the amount of male RE because males invest disproportionately in nest building, courtship feeding, and other behaviors that may not be directly associated with increased confidence of paternity. Male snail kites do not guard their mates extensively, and females are often left undefended in the nest area for substantial periods while males fly 1–3 km away in search of snails for their mates or sticks for nest building. Confidence of paternity is probably high, however, because unguarded females never solicited copulations nor were they successfully forced to copulate with nearby males, whether in the proximity of the nest or not. Females may be unwilling to copulate with intruding males in order to protect the investment of their mate and thereby prevent early mate desertion (Gladstone 1979). In summary, high male investment during the prezygotic period may contribute to increased confidence of paternity, but it is unlikely to be the major purpose or cause of this behavior.

The male response to females requiring large investments before egg laying could be desertion. But all males invest to varying degrees in courtship feeding, and because this ME activity is not generalizable (Low 1978), it cannot be directed to another female to secure additional matings. By deserting a "coy" mate before egg laying, males forfeit their ME investments in hopes of finding "faster" females with less associated investment. This strategy has two dangers. First, male success in finding a fast female depends on the relative proportion of females that employ fast and coy strategies (Dawkins 1976; Maynard Smith 1982). If females using the "heavy male investment" strategy are favored because of their ability to recycle clutches, coy females would then predominate and males would soon have little choice but to invest. Second, fast females are probably associated with a decreased confidence of paternity, which males should avoid (Trivers 1972). To avoid being cuckolded, males may accept longer periods of pair formation (Zenone et al. 1979) and, in the process, incur higher RE costs than females.

Differences in relative past investment by the sexes not only influence mate-desertion behavior but also have been thought to control the operation of sexual selection and the evolution of sexual differences. "The sex whose typical parental investment is greater than that of the opposite sex will become a limiting resource for that sex" (Trivers 1972, p. 140), resulting in competition among members of the sex investing less (usually males) to mate with the sex investing more (usually females). In snail kites, however, it is not clear which sex can be a limiting resource on the basis of the RE expended because, depending on which one deserts its mate, either sex may invest more total RE in a reproductive bout (Beissinger 1984; Beissinger and Snyder 1987). On the basis of prezygotic investments, one might expect snail kite females to be more sexually competitive than

males; however, the males appear to compete more extensively for mates via display flights, chases, and courtship feeding.

The snail kite example shows a potential problem with Trivers' (1972) sex-difference theory: for the sex investing less, competing for a mate causes prezygotic investment (ME) to rise. If intrasexual competition by the sex investing less takes a form that the other sex can use as PE to increase offspring production (e.g., courtship feeding of females by male snail kites), then selection could act on the competing sex to increase its ME to such a degree that its total prezygotic effort may exceed that of the other sex (as in fig. 4). This should particularly occur when ME is not generalizable from one potential mate to another because under these circumstances male and female interests complement each other. When male and female interests during the prezygotic period are symmetrical rather than conflicting, selection on the allocation of RE by the sexes could reach a stable equilibrium at which the competitive sex may invest more than its mate. Gwynne's (1981) studies of female Mormon crickets (*Anabrus simplex*) competing for spermatophore-donating males may be another example of this phenomenon.

In conclusion, by withholding energy investments and causing male prezygotic RE to exceed their own, female snail kites have overcome the immediate effects of anisogamy (unequal investment and opportunity costs). The extent to which females regularly overcome anisogamy in other organisms remains to be seen. Although some poikilothermic males invest significant amounts of ME via spermatophores or courtship feeding (e.g., Thornhill 1976, 1981; Boggs and Gilbert 1979; Gwynne 1981), the cost to males of courtship activities may be insufficient to exceed prezygotic investments by females on a regular basis because the basal metabolic rate and activity costs in cold-blooded animals are much lower than in homoiotherms (Bartholomew 1982), and the length of time required for courtship may often be much shorter. In homoiotherms, however, females may regularly overcome the immediate effects of anisogamy because the costs of securing copulations for males of many species are probably substantial on account of the potentially longer courtship periods and higher metabolic expenditures for courtship activities. Finally, females may be expected to overcome anisogamy on a regular basis in species for which the expenditure of RE by a male on one female is not generalizable to another and can be converted by females into PE (e.g., courtship feeding).

SUMMARY

It has often been suggested that, because of anisogamy, females are likely to have invested more reproductive effort (RE) than males at the moment of fertilization. The energy and risk incurred by snail kite parents from pair formation through egg laying was assessed using time-activity budgets and reproductive bioenergetics. Males contributed significantly more to nest building and to chasing potential predators and conspecifics; they spent significantly more time foraging for their mates and for themselves, providing, on the average, 83% of the female's food; and they expended nearly twice as much energy as females. Including the cost of clutch production, models of cumulative energy expenditure as estimates

of RE based on rapid or slow pair formation indicate that males consistently invested more energy than females through the time of egg laying.

RE by female snail kites is lower than that of males because females pursue a strategy of decreasing energy demands during egg laying by decreasing locomotor activity. Withholding energy investments may allow females to avoid energy depletion during egg laying and permit increased iteroparity; this strategy should be highly favored because both nest-failure rates and environmental uncertainty are high. A large initial investment by males before egg laying may contribute to an increased confidence of paternity but is more likely to be a result rather than the cause of females' overcoming the immediate costs of anisogamy. Snail kites also exemplify a class of exceptions to Trivers' (1972) theory of sexual differences, whereby the sex competing for mates is predicted to be the one investing less RE.

LITERATURE CITED

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

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

Ankney, C. D. 1977. The use of nutrient reserves by breeding male lesser snow geese, *Chen caerulescens caerulescens*. Can. J. Zool. 55:1984–1987.

Bartholomew, G. A. 1982. Energy metabolism. Pages 57–110 *in* M. S. Gordon, ed. Animal physiology: principles and adaptations. Macmillan, New York.

Beecher, M. D., and I. M. Beecher. 1979. Sociobiology of bank swallows: reproductive strategy of the male. Science (Wash., D.C.) 205:1282–1285.

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

———. 1984. Mate desertion and reproductive effort in the snail kite. Ph.D. diss. University of Michigan, Ann Arbor.

———. 1986. Demography, environmental uncertainty and the evolution of mate desertion in the snail kite. Ecology 67:1445–1459.

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

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

Bent, A. C. 1937. Life histories of North American birds of prey. U.S. Natl. Mus. Bull. 167:70–78.

Birkhead, T. R. 1979. Mate guarding in the magpie *Pica pica*. Anim. Behav. 27:866–874.

Boggs, C. L., and L. E. Gilbert. 1979. Male contribution to egg production in butterflies: evidence for transfer of nutrients at mating. Science (Wash., D.C.) 206:83–84.

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

Brody, S. 1945. Bioenergetics and growth. Reinholt, New York.

Burger, J. 1981. Sexual differences in parental activities of breeding black skimmers. Am. Nat. 117:975–984.

Carey, D. M. 1985. Climatological and environmental factors effecting the foraging behavior and ecology of the snail kite (*Rostrhamus sociabilis plumbeus* Ridgeway). Master's thesis. University of Miami, Coral Gables, Fla.

Chandler, R., and J. M. Anderson. 1974. Notes on everglade kite reproduction. Am. Birds 28:856–858.

Daly, M., and M. Wilson. 1983. Sex, evolution and behavior. 2d ed. Willard Grant Press, Boston.

Dawkins, R. 1976. The selfish gene. Oxford University Press, Oxford.

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

Dewsbury, D. A. 1982. Ejaculate cost and male choice. Am. Nat. 119:601–610.

Drobney, R. D. 1980. Reproductive bioenergetics of wood ducks. Auk 97:480–490.

Fisher, R. A. 1930. The genetical theory of natural selection. Dover, New York.

Gadgil, M., and W. H. Bossert. 1970. Life history consequences of natural selection. Am. Nat. 104: 1–24.

Gladstone, D. E. 1979. Promiscuity in monogamous colonial birds. Am. Nat. 114:545–557.

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

Gwynne, D. T. 1981. Sexual difference theory: Mormon crickets show role reversal in mate choice. Science (Wash., D.C.) 213:779–780.

Haverschmidt, F. 1962. Notes on the feeding habits and food of some hawks of Surinam. Condor 64:154–158.

Hirschfield, M. F., and D. W. Tinkle. 1975. Natural selection and the evolution of reproductive effort. Proc. Natl. Acad. Sci. USA 72:2227–2231.

Horowitz, W., ed. 1970. Official methods of analysis of the Association of Official Analytical Chemists. 11th ed. Association of Official Analytical Chemists, Washington, D.C.

Howell, A. H. 1932. Florida bird life. Coward-McCann, New York.

Kendeigh, S. C., V. R. Dol'nik, and V. M. Gavrilov. 1977. Avian energetics. Pages 127–204 *in* J. Pinowski and S. C. Kendeigh, eds. Granivorous birds in ecosystems. Cambridge University Press, New York.

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

Krapu, G. L. 1981. The role of nutrient reserves in mallard reproduction. Auk 98:29–38.

Krebs, J. R. 1970. The efficiency of courtship feeding in the blue tit *Parus caeruleus*. Ibis 112:108–110.

Kushlan, J. A. 1975. Population changes of the apple snail, *Pomacea paludosa*, in the southern Everglades. Nautilus 89:21–23.

Lack, D. 1940. Courtship feeding in birds. Auk 57:169–178.

Low, B. S. 1976. The evolution of amphibian life histories in the desert. Pages 149–195 *in* D. W. Goodall, ed. Evolution of desert biota. University of Texas Press, Austin.

———. 1978. Environmental uncertainty and the parental strategies of marsupials and placentals. Am. Nat. 112:197–213.

Maynard Smith, J. M. 1982. Evolution and the theory of games. Cambridge University Press, London.

Montevecchi, W. A., and J. M. Porter. 1980. Parental investments by seabirds at the breeding area with emphasis on northern gannets (*Morus bassanus*). Pages 323–365 *in* J. Burger, B. L. Olla, and H. E. Winn, eds. Behavior of marine animals. Vol. 4. Marine birds. Plenum, New York.

Nakatsuru, K., and D. L. Kramer. 1982. Is sperm cheap? Limited male fertility and female choice in lemon tetra (Pisces, Characidae). Science (Wash., D.C.) 216:753–755.

Nicholson, D. J. 1926. Nesting habits of the everglade kite in Florida. Auk 43:62–67.

Nisbet, I. C. T. 1973. Courtship-feeding, egg-size, and breeding success in the common tern (*Sterna hirundo*). Nature (Lond.) 241:141–142.
———. 1977. Courtship-feeding and clutch size in common terns *Sterna hirundo*. Pages 101–109 *in* B. Stonehouse and C. Perrins, eds. Evolutionary ecology. University Park Press, Baltimore, Md.
Partridge, L., and T. Halliday. 1984. Mating patterns and mate choice. Pages 222–250 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. 2d ed. Blackwell, Oxford.
Power, H. W. 1980. Male escorting and protecting females at the nest cavity of mountain bluebirds. Wilson Bull. 92:509–511.
Ricklefs, R. E. 1974. Energetics of reproduction in birds. Pages 152–292 *in* R. A. Paynter, ed. Avian energetics. Nuttall Ornithological Club, Cambridge.
Ridley, M. 1978. Paternal care. Anim. Behav. 26:904–932.
Royama, T. 1966. A reinterpretation of courtship feeding. Bird Study 13:116–129.
Sarker, S. U., and G. Naulleau. 1981. Étude quantitative des fientes et de l'assimilation chez les Rapaces. Oiseau Rev. Fr. Ornithol. 51:161–165.
Snyder, N. F. R., and H. W. Kale II. 1983. Mollusc-predation by snail kites in Colombia. Auk 100: 93–97.
Snyder, N. F. R., and H. A. Snyder. 1969. A comparative study of mollusc predation by limpkins, everglade kites and boat-tailed grackles. Living Bird 8:177–233.
Stearns, S. C. 1976. Life-history tactics: a review of the ideas. Q. Rev. Biol. 51:3–46.
Steel, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill, New York.
Sykes, P. W., Jr. 1983. Snail kite use of the freshwater marshes of south Florida. Fla. Field Nat. 11: 73–88.
Sykes, P. W., Jr., and H. W. Kale II. 1974. Everglades kites feed on nonsnail prey. Auk 91:818–820.
Thornhill, R. 1976. Sexual selection and paternal investment in insects. Am. Nat. 110:153–163.
———. 1981. *Panorpa* (Mecoptera: Panorpidae) scorpionflies: systems for understanding resource-defense polygyny and alternative male reproductive efforts. Annu. Rev. Ecol. Syst. 12:355–386.
Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136–179 *in* B. Campbell, ed. Sexual selection and the descent of man, 1871–1971. Aldine, Chicago.
———. 1985. Social evolution. Benjamin/Cummings, Menlo Park, Calif.
Walsberg, G. E. 1983. Avian ecological energetics. Avian Biol. 7:161–220.
Weathers, W. W., W. A. Buttemer, A. M. Hayworth, and K. A. Nagy. 1984. An evaluation of time-budget estimates of daily energy expenditures in birds. Auk 101:459–472.
Werschkul, D. F. 1982. Parental investment: influence of nest guarding by male little blue herons *Florida caerulea*. Ibis 124:343–346.
Williams, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, N.J.
Williams, J. B., and K. A. Nagy. 1984. Daily energy expenditure of savannah sparrows: comparison of time-energy budget and doubly-labeled water estimates. Auk 101:221–229.
Wilson, E. O. 1975. Sociobiology. Harvard University Press, Cambridge, Mass.
Wittenberger, J. F. 1981. Animal social behavior. Wadsworth, Belmont, Calif.
Yamagishi, S., and M. Saito. 1985. Function of courtship feeding in the bull-headed shrike, *Lanius bucephalus*. J. Ethol. 3:113–121.
Zenone, P. G., M. E. Sims, and C. J. Erickson. 1979. Male ring dove behavior and the defense of genetic paternity. Am. Nat. 114:615–626.