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DEMOGRAPHY, ENVIRONMENTAL UNCERTAINTY, AND THE EVOLUTION OF MATE DESERTION IN THE SNAIL KITE¹

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Abstract. The Snail Kite (*Rostrhamus sociabilis*), an endangered hawk, has a unique mating system in Florida (Beissinger and Snyder 1987): when food is abundant, males or females desert their mates at nearly equal frequency (ambisexual mate desertion) in the midst of a nesting cycle. I examined the demographic and environmental constraints selecting for a clutch size that permits one parent to desert, yet optimizes the number of offspring produced by each parent. Demographic studies, conducted from 1979-1983, indicated that kites have (1) a very high nest failure rate ($\bar{X} = 68\%$) due most often to unstable nest sites and predation, (2) a variable nesting season (5-10 mo/yr), (3) an early age of first reproduction for a bird this size (10 mo), (4) a high degree of iteroparity (double and potentially triple clutching within a season), and (5) unstable populations. Both nesting success and population size were directly related to Everglades water levels and resultant snail densities. Kites responded to large annual changes in food abundance, not by adjusting clutch size but by deserting their mates and presumably attempting to renest.

Kite demographic traits appear to be adaptations to or results of an uncertain environment. Based on 67 yr of Everglades water levels, environmental predictability, measured by spectral analysis and Colwell's (1974) index, was low and influenced by water management regimes: (1) water levels were lowered, (2) annual variation in levels increased and annual cycles became stronger, (3) the period length of long-term drought-flood cycles shifted from 10 or more yr toward 5 yr, and (4) levels became a less predictive cue for favorable nesting conditions.

A potential evolutionary pathway from biparental care to mate desertion in Snail Kites is proposed. It is unlikely that mate desertion evolved solely from a context of conflict between the sexes, because kite nesting success is so low that it is probably maladaptive for a parent to desert and jeopardize the survival of any of its first brood. Instead, mate desertion behavior probably evolved in response to a smaller average clutch size; this would allow females to be highly iteroparous and avoid the costs of overinvestment, and should be strongly favored in a highly uncertain environment. Analysis of clutches in museum collections suggests that an apparent decline in clutch size may have occurred in Florida during the past century. The potential for ambisexual mate desertion to occur in other vertebrates is examined.

Key words: *demography; endangered species; environmental predictability; Florida Everglades; life history strategies; mate desertion; mating systems; parental care; polygamy; reproductive biology; Snail Kite (Rostrhamus sociabilis).*

INTRODUCTION

A mating system is the sum of the outcomes of "decisions" by individuals, presumably selected to maximize their lifetime reproductive successes (fitnesses). An individual may decide upon the number of mates, manner in which they are acquired, characteristics of pair bonds, and patterns of parental care it will provide (Emlen and Oring 1977). The possible outcomes of these decisions, or strategies of individuals, are subject to environmental and phylogenetic constraints that may limit choice to several alternatives (Oring 1982). As in any form of social behavior, the best set of alternatives, the evolutionarily stable strategy (ESS; Maynard Smith and Price 1973, Maynard Smith 1977), depends not

only upon these constraints but also upon the behavior of other members of the population.

Mating systems of most vertebrates are characterized by mate desertion by one sex (but see Davies 1985), often leading to polygyny or polyandry (Kleiman 1977, Ridley 1978, Perrone and Zarrett 1979, Wells 1981). In birds, however, mate desertion is especially rare and most species are monogamous, with biparental care (Lack 1968, Oring 1982). The Snail Kite (*Rostrhamus sociabilis*), a medium-sized hawk that nests in loose colonies and is renowned for its specialized diet of large freshwater *Pomacea* snails (Howell 1932:168-171, Haverschmidt 1962, Snyder and Snyder 1969, and others in Beissinger, *in press*), has a mating system in Florida that appears to be unique (Beissinger 1984, Beissinger and Snyder 1987). Either males or females may desert their mates in the midst of a breeding cycle (ambisexual mate desertion). Offspring mortality, however, rarely occurs after desertion. The occurrence of desertion in Snail Kites is related to food abundance; when snails are abundant, individuals are likelier to

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desert. Males and females desert their mates at nearly equal frequency. By deserting, individuals escape parental duties, save reproductive effort, and can possibly renege during the long breeding season. The mates that remain ("tenders") nearly always successfully finish rearing the young alone at what seems likely to be a substantial cost to them in fitness. Ambisexual mate desertion leading to polygamy is not known to occur regularly in other vertebrates (see Solheim 1983 for a possible example) and therefore requires an explanation.

Mating systems theory has focused on the environmental potential for polygamy and the ability of a portion of members of one sex to monopolize resources and mates (Orrians 1969, Emlen and Oring 1977, Wittenberger 1981, Oring 1982). Models of parental or reproductive investment also have been used to explain the evolution of mating systems in general and mate desertion in particular (Trivers 1972, Dawkins and Carlisle 1976, Boucher 1977, Maynard Smith 1977, 1982, Grafen and Sibly 1978). But these models do not explain why it is advantageous for Snail Kites to produce broods small enough to be deserted by one parent without losing any young, instead of larger broods requiring biparental care throughout the nesting cycle.

The purpose of this paper is to explore the probable evolutionary pathways that lead to ambisexual mate desertion in Snail Kites by examining the environmental and demographic constraints leading to selection for a clutch size that permits one adult to desert, yet optimizes the number of offspring produced by a parent. I also discuss why either sex is capable of mate desertion in the Snail Kite, and what life history characteristics are likely to lead to ambisexual mate desertion in other parental organisms.

STUDY AREAS AND ENVIRONMENTAL CONDITIONS

Snail Kite nesting activity was monitored from 1979–1983 throughout southern Florida wetlands: Lake Okeechobee (Glades, Hendry, Okeechobee, and Palm Beach counties), State Water Conservation Area 3A (CA3A) (Dade and Broward counties), and CA2 (Broward County). The latter two areas comprise nearly all of the modern Everglades habitat, and all three areas have been used frequently by kites during the last decade. Sykes (1979, 1983a), Beissinger and Takekawa (1983), Beissinger (1984), and Beissinger and Snyder (1987) describe these habitats and their use by kites during the study period.

From 1978–1980, Snail Kites nested mostly in CA3A and Lake Okeechobee. But in 1981 southern Florida experienced severe drought. Nearly all of the wetlands customarily used by kites were dry from May–August 1981 and again from April–May 1982. Kite use, water levels, and habitat changes during this period are described in detail in Beissinger and Takekawa (1983). In 1982, nesting occurred only in two small populations, newly established on Lakes Tohopekaliga and

Kissimmee (Osceola County). After CA3A had been flooded continuously for nearly a year, most kites returned there to nest in 1983 and in adjoining northern sections of Everglades National Park (Dade County; Kushlan and Bass 1983).

METHODS

I studied the nesting biology and demography of Snail Kites from January through August 1979, 1981, and 1982, in July and August 1980, and from March through June in 1983. Study areas were traversed by airboat at least weekly in search of nesting kites. Nests were located by observing the behavior of adults (Beissinger, *in press*) and later marked with plastic tags for identification. Thereafter, nest contents were checked biweekly, weekly, or bimonthly, often with a mirror on an extension pole, to determine the fate of the nest, and the timing and inferred cause of nest failure. Effort was made to minimize the disturbance of nesting parents by limiting the frequency and duration of nest checks. See Beissinger (1984) and Beissinger and Snyder (1987) for details on the methodology used to detect and monitor nests for mate desertion.

Environmental variability and predictability were determined using 67 yr (1916–1982) of end-of-the-month water levels of Lake Okeechobee (the mean of three gauge readings taken in height above mean sea level [MSL]) obtained from the United States Geological Survey, Miami Field Office (Fig. 3). The Lake Okeechobee data are the longest continual set of water measurements in southern Florida. Although Lake Okeechobee water levels may be controlled separately from levels in the southern Everglades, lake levels are probably indicative of general conditions in the Everglades. Also, Snail Kite numbers are strongly correlated with Lake Okeechobee water levels (Sykes 1983b).

To analyze historical changes, years were grouped into three eras based on water management practices: Predrainage (1916–1930), Drainage (1931–1961), and Modern (1962–1982). Even though some of the dikes on Lake Okeechobee and Everglades canals were completed or under construction during the Predrainage period, most were not fully operational and did not effectively drain wetlands (Parker et al. 1955, Brooks 1974, Parker 1974, Blake 1980). Lake water levels were not effectively controlled during Predrainage, although they do appear lower than some pre-1900's estimates (Tebeau 1971, Brooks 1974, Parker 1974). During the Drainage period, Hoover dike was completed around Lake Okeechobee and the major Everglades drainage canals became operational. Drainage was fullscale, lake levels were "controlled," and a maximum regulation schedule (maximum level) of 4.72 m above MSL was set. The Modern period of water management began when construction projects on Lake Okeechobee and the State Water Conservation Areas were completed and managed as a unit. During this period, the max-

imum regulation schedule remained at 4.72 m above MSL until 1974, when it was raised to 4.88 m above MSL. Subsequently in 1978 it was raised to 5.33 m above MSL.

Spectral analysis (Jenkins and Watts 1968:243-257, Kendall 1976) was used to examine cycles in Lake Okeechobee water levels. Spectral density was estimated using a Parzen2 window applied to a maximum lag for the autocorrelation function of 100 observations or one-fourth of the sample size, whichever was less. The assumption of a weakly stationary timeseries of equally spaced time points was not violated.

Colwell's environmental predictability index (Colwell 1974, Low 1978, 1979, Stearns 1981, Zammuto and Millar 1985) was calculated using Fortran computer programs on the Michigan Terminal System developed by Jacquez (1983). Four water level states were chosen based on 10 yr of Snail Kite nesting success studies on Lake Okeechobee under each regime (R. Chandler, *personal communication*, N. F. R. Snyder, *personal communication*, S. R. Beissinger, *personal observation*): (1) Poor (2.96-3.96 m [9.7-13.0 ft] above MSL), when nesting was rarely successful because most of the wetlands were dry; (2) Marginal (3.96-4.42 m [13.0-14.5 ft] above MSL), when nesting was mostly in cattails (*Typha* sp.) and success was poor to fair as few shrub nest sites were flooded; (3) Good (4.42-5.03 m [14.5-16.5 ft] above MSL), when all wetlands and potential nest sites were flooded; and (4) Good With Storage (5.03-5.73 m [16.5-18.8 ft] above MSL), when all potential nest sites were available and water was stored or historically overflowed slowly into the Everglades, prolonging the hydroperiod (Parker 1974). By combining the last two states into one state representative of water levels favoring successful nesting by kites, Colwell's index of predictability also was calculated for three water level states. Each month was considered a season because: (1) active kite nests have been found in every month in Florida (Beissinger, *in press*), indicating that kites must assess water levels and other environmental variables often in deciding when to nest; (2) water level records primarily are avail-

TABLE 1. Summary of Snail Kite nesting attempts and water levels in Florida from 1978 to 1983. Successful nests fledged at least one young. Unpublished data from 1978-1979 courtesy of Noel F. R. Snyder and Roderick Chandler. Excluded from nest success analyses were nests with a high potential for failing that were placed in Chandler nest baskets to ensure success (R. Chandler and S. R. Beissinger, *personal observations*) and nests found after hatching.

Year	No. nests	No. success-ful	Percent success-ful	Water levels	Season (no. months)
1978	100	40	40	high	10
1979	131	54	41	high	9
1981	12	0	0	low	5
1982	40	2	5	low	7
1983	48	10	21	high	9

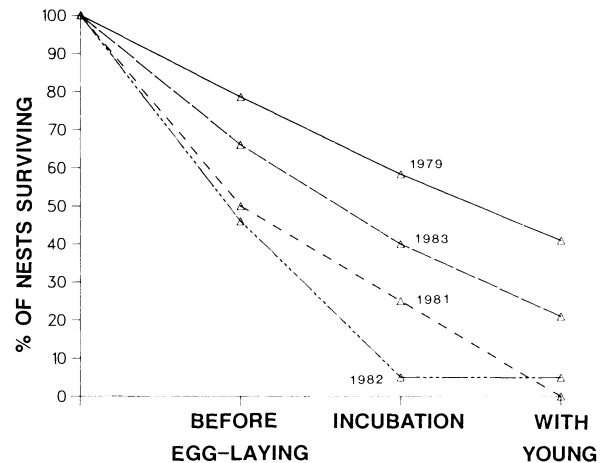


FIG. 1. Survivorship curves for Snail Kite nests throughout the nest cycle by year of study.

able as monthly data, especially records before 1932; (3) combining months without knowledge of the pattern of seasonality might obscure relationships; and (4) calculations of Colwell's index of predictability for Lake Okeechobee water levels yielded very little variation when the number of seasons was varied from 3 to 12.

Records of Snail Kite clutches were solicited from 85 museums and private collections in North America, Latin America, and Europe for analyses of latitudinal and historical trends. Data from certain collectors of large clutches (4 or more eggs) who had a history of altering clutches or fabricating data were eliminated from these analyses (identified by Lloyd Kiff, Western Foundation of Vertebrate Zoology).

RESULTS

Snail Kite demographics

Nest success for Snail Kites in Florida varied greatly from year to year but overall was low (Table 1). Only 32% of 331 nests fledged at least one young. The 5-yr average annual success rate was even lower, $21 \pm 19\%$, and average nest success would have been even smaller had many imperiled nests not been placed into Chandler nest baskets (Sykes and Chandler 1974, R. Chandler and S. R. Beissinger, *personal observations*). Sykes's (1979) estimate of 48% nest success for Florida kites was inflated by the inclusion of many basketed nests and exclusion of some nests that failed before egg-laying. Nest success also differed significantly among years ($\chi^2 = 27.0$, $df = 4$, $P < .001$), ranging from 0-5% in the 1981 and 1982 drought years to 40-41% during the wet years of 1978 and 1979.

The timing of nest failure (Fig. 1, Table 2) varied significantly among years ($\chi^2 = 13.74$, $df = 4$, $P = .01$). Failure occurred frequently before the eggs were laid, especially during dry years (1981, 1982) when nests were often placed in structurally weak sites (e.g., cattails). Inclement weather conditions (e.g., cold fronts)

TABLE 2. The timing and cause of nest failure for Snail Kite nests in Florida by year of study. Nests placed in Chandler nest baskets were not included. See Table 1 for sample sizes of nests for each year.

	Year of study				Mean \pm SE
	1979	1981	1982	1983	
Timing	Percent of nest failures				
Before egg-laying	29	33	53	34	37 \pm 5
With eggs	26	17	39	26	27 \pm 5
With young	21	17	0	19	14 \pm 5
Unknown	24	33	8	21	21 \pm 5
Cause					
Predation	20	0	11	25	14 \pm 5
Structural failure	14	31	39	18	26 \pm 5
Unknown	63	46	50	48	52 \pm 4
Infertile eggs	3	0	0	2	1 \pm 1
Desertion	0	15	0	2	4 \pm 4
Other*	0	8	0	5	3 \pm 2

* Includes attacks by ants and a male unable to secure a mate.

also may be responsible for some nest desertion before the eggs are laid. During wet years (1979, 1983), nearly half of the nesting attempts failed between egg-laying and fledging.

Analysis of the inferred causes of nest failure was inconclusive (Table 2). Structural collapse of nests due to poor nest substrate, wind, or changes in water level was the most frequently identified cause of failure and occurred more often during dry years when kites nested in lake habitats (R. Chandler and S. R. Beissinger, *personal observations*). Predation also was an important cause of nest failure in some years. Predators of kite eggs included Boat-tailed Grackles (*Quiscalus ma-*

ja), Florida cottonmouths (*Agkistrodon piscivorus conanti*), and Everglade rat snakes (*Elaphe obsoleta rossalleni*). In addition, both of these snake species, Northern Harriers (*Circus cyaneus*), and raccoons (*Procyon lotor*) probably eat nestlings. Nest success was particularly poor when water levels were low or falling (Table 1) and the marsh dried out beneath nests; failure occurred at seven of nine such nests during 1981–1983. Predation caused the failure of three, one was deserted, and the cause of failure in the other three was unknown; predation reduced the broods of the only two successful nests, which had been placed in Chandler nest baskets. These data suggest that predator avoidance may well be the reason why Snail Kites always select nest sites over water.

Unlike nesting success, reproductive output by successful kite pairs varied little among years (Fig. 2). There was no significant change in mean clutch size ($F_{3,154} = 0.35$, $P > .78$), modal clutch size (three in all years), or the distribution of clutch sizes among years ($\chi^2 = 6.5$, $df = 9$, $P > .60$) despite large year-to-year variation in snail abundances, which were directly related to changes in water levels (Beissinger and Snyder 1987). An average of two young was produced per successful nest in all years, similar to an average of 1.9 young per successful nest in the mid-1970's (Sykes 1979).

Fledgling Snail Kites are no longer dependent upon their parents for care by ≈ 10 wk of age. Postfledging survival is difficult to estimate because kites, even young ones, may move great distances in a season. In telemetry studies of 13 fledglings from six nests in 1979, all survived for > 1.5 yr (the life of the transmitters). Thus, postfledging survival may be quite high in years when snail abundance and water levels are adequate. During drought years, however, postfledging success is probably much lower. In 1981, only two of four young survived for at least 2 mo postfledging at the only two successful nests on Lake Okeechobee.

Snail Kites in Florida are capable of reproducing at a very young age: 10 cases of banded 1-yr-old kites nesting, both males and females, have been documented (N. F. R. Snyder, R. Chandler, and S. R. Beissinger, *personal observations*). The youngest was a female that laid a clutch at 10 mo of age. These data are contrary to estimates of 3 yr for age of first reproduction by Sykes (1979) and Nichols et al. (1980).

Breeding seasons in Florida vary greatly in duration (Table 1). Active nests have been reported in each month and the breeding season may shift calendar position from year to year (Beissinger, *in press*). Longer breeding seasons, extending up to 10 mo (December–October), occurred during wet years, but dry years may restrict nesting to 5 mo (March–July). A large portion (estimated 80–90%) of the population did not even attempt to nest during the 1981 drought.

During wet years, kites may regularly attempt to raise more than one brood in a breeding season. Seven in-

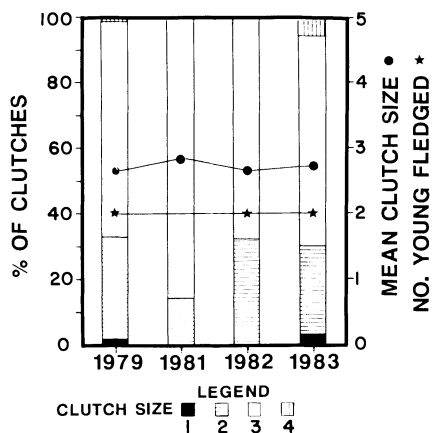


FIG. 2. Snail Kite reproductive output by year of study in Florida: the percent of nests that had each clutch size (shown by height of the respective bar segment), mean clutch size, and mean number of young fledged per successful nest. Numbers of clutches are 90 (1979), 7 (1981), 28 (1982), and 33 (1983). See Table 1 for the number of nests successfully fledging young in each year.

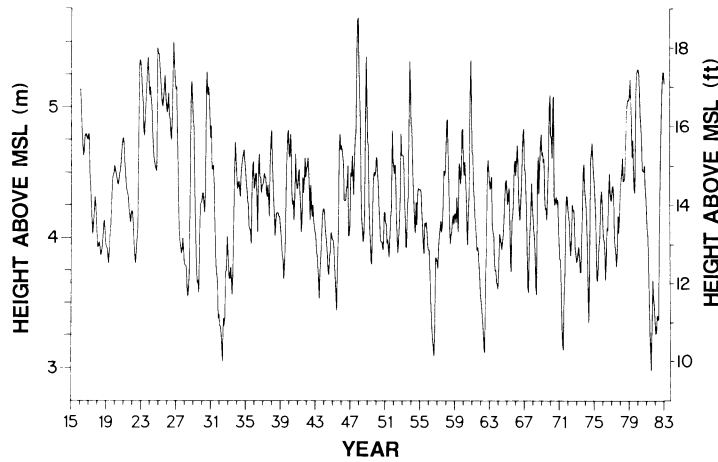


FIG. 3. Lake Okeechobee surface water elevation from 1916–1982. The end-of-the-month reading for this 67-yr data set is expressed as height above mean sea level (MSL) as measured by the United States Army Corps of Engineers (see Methods).

stances of double brooding (three of which successfully fledged young) were recorded from resightings of birds that were banded ($N = 5$) or had clearly recognizable plumage characteristics ($N = 2$). It is difficult to document the frequency of re-pairing and re-nesting due to the mobility of Snail Kites (e.g., one re-nesting occurred 160 km from the previous site) and the difficulties in following them or relocating them in the thousands of square kilometres of Everglades. Nevertheless, attempted re-nesting within a season was detected for 5 of 14 cases (30%) in which banded birds successfully fledged first broods early enough in the breeding season to allow re-nesting. Re-nesting immediately following nest failure (<10 d) also was recorded for two females that failed early in the season. Thus, it is likely that a high degree of re-nesting can occur during years of favorable water conditions.

In Florida, kites appear to be long lived, but estimates of adult survival are vague due to few recoveries of mortalities and the mobility of banded birds. Maximum known ages of birds in the wild ranged from 7 to 8.8 yr (Sykes 1979) and 11 to 13 yr (this study). In captivity, some individuals of the South American race reached 15 yr of age and were still able to reproduce (G. F. Gee, *personal communication*). Under most conditions, adult mortality due to predation is rare. Probably the main source of mortality for adults in Florida is regional drought, which on the average occurs every 5–7 yr (see Environmental Variability and Predictability). During drought conditions, snails become unavailable to kites, which results in massive dispersal by kites (Beissinger and Takekawa 1983), and populations may decline 50% or more (Sykes 1979, Beissinger 1984). For instance, the Florida kite population declined from 651 birds in December 1980 (Sykes 1983b) to ≈ 250 birds by March 1982 during a severe drought. Thus, although Snail Kites have the potential to be relatively long lived, adult lifespans in

Florida may average only 5–8 yr, the interdrought interval.

Because cyclic drought in Florida causes high adult mortality and low recruitment, kite populations are quite unstable. Analyses of population trends in Florida (Sykes 1979, 1983b, Beissinger 1984) indicate that Snail Kites can have a relatively high intrinsic rate of increase under wet conditions (0.51–0.61) and a similar potential for population decline during dry conditions. Because changes in kite numbers and distribution are related directly to Everglades water levels (Beissinger and Takekawa 1983, Sykes 1983a, 1983b), and kite nest success may be affected directly by changes in water depth, the variability and predictability of Everglades water levels are important for Snail Kites.

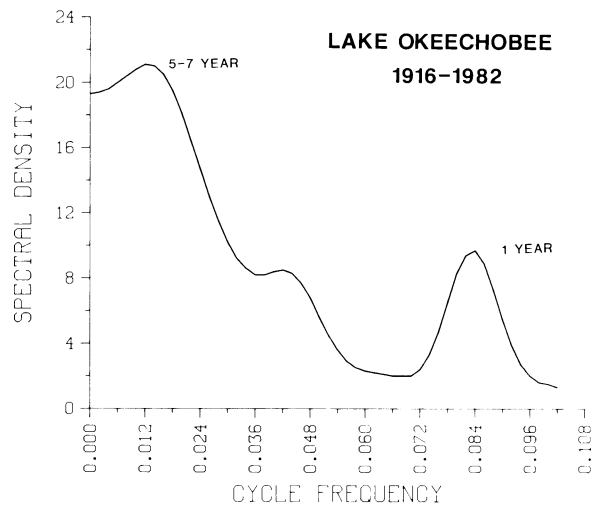
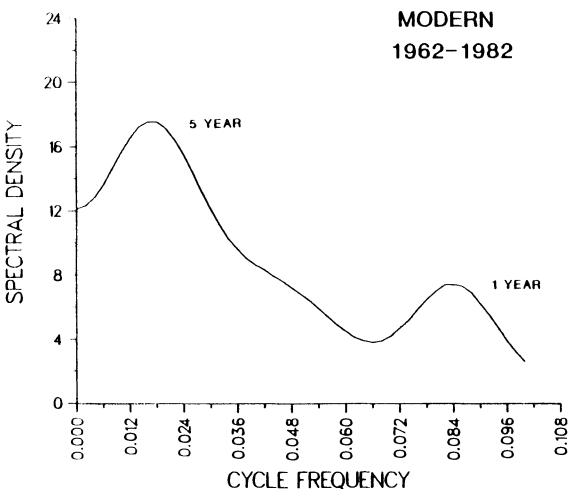
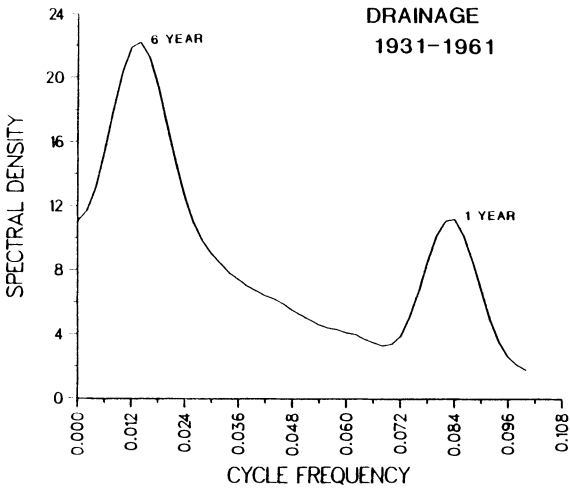
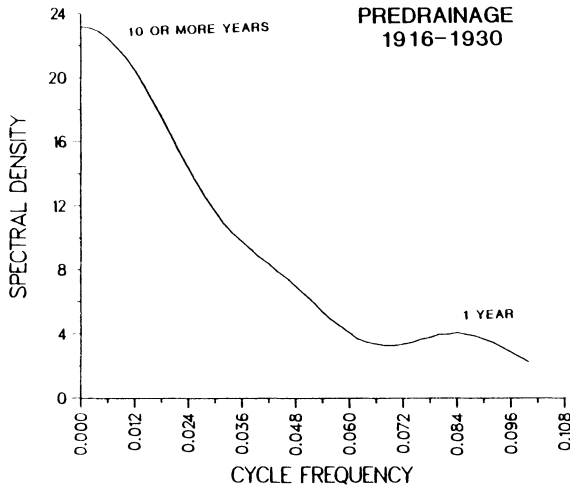


FIG. 4. Spectral analysis of Lake Okeechobee surface water elevation from 1916–1982. The annual cycle and 5–7 yr drought–flood cycle are indicated. The spectral density is a measure of intensity of a cycle at a given frequency. Cycle frequency is the inverse of the number of months considered.



Environmental variability and predictability

A data set of 67 yr of monthly water level records for Lake Okeechobee (Fig. 3) was analyzed for variability, predictability, and historic trends. Based on spectral density (Kendall 1976), a measure of the intensity of a cycle at a given frequency, there are two cycles in water levels (Fig. 4): a weaker annual (short) cycle resulting from the effects of annual wet and dry seasons, and a strong long-term cycle of 5-7 yr resulting from periodic droughts and floods. This long-term cycle in lake levels is similar to a 5-7 yr rainfall cycle for the Kissimmee River basin, the major source of Lake Okeechobee water (W. C. Huber, *personal communication*).

The strength and frequency of Lake Okeechobee water level cycles changed during the 67-yr period of record (Fig. 5). First, the annual cycle, which was relatively weak during the Predrainage period, increased significantly during Drainage (one-tailed *F* test for spectral densities at 12 mo, Jenkins and Watts 1968:243-257; $F_{15,15} = 2.64, P < .05$), then dropped to a nonsignificant difference ($F_{15,15} = 1.86, P > .10$) during the Modern period of water management. The annual cycle represents a measure of seasonality or contingency in Colwell's (1974) terminology. Second, the long-term cycle may have gradually become shorter, diminishing from a longer cycle (10 or more yr) in the early 1900's before drainage to a 6-yr cycle during the middle 1900's, and finally shifting towards a 5-yr cycle in the past 23 yr.

Environmental predictability also was analyzed using Colwell's index (1974) where predictability (*P*) varies from 0 (unpredictable) to 1 (predictable) and is the sum of two components: constancy (*C*) or the degree of variability through time of a particular state, and contingency (*M*), which measures the probability through time that each environmental state is dependent on another environmental state (i.e., seasonality). Conclusions from Colwell's index (Table 3) are similar to those derived from spectral analysis. Recognizing four water level states (see Methods), predictability (*P*) of Lake Okeechobee water levels was low before drainage, increased strongly during Drainage, and decreased to an intermediate value during the Modern period. Changes in contingency (*M*) were similar to changes in the annual cycle shown by spectral analyses (Fig. 5). The changes in predictability, however, were due mainly to changes in constancy (*C*); water levels became constantly lower, resulting in less favorable water levels for Snail Kite nesting. There was a significant change ($\chi^2 = 83.4, df = 6, P < .001$) in the frequency of observations in each state (Table 3), shifting away from

FIG. 5. Spectral analysis of Lake Okeechobee surface water elevation for comparison of the intensity of the annual cycle and drought-flood cycle among three water management eras in Florida. Terms are defined in Fig. 4 legend.

TABLE 3. Analysis of Colwell's (1974) environmental predictability index for Lake Okeechobee end-of-the-month lake stage readings in metres above mean sea level. Three or four water level states were chosen based on past studies of Snail Kite nesting success under each regime (see Methods).*

Water management practice	Observations in each Lake Okeechobee water level state													
	Predictability index						Poor		Marginal		Good		Good with storage	
	Three states			Four states			No.	%	No.	%	No.	%	No.	%
	<i>P</i>	<i>M</i>	<i>C</i>	<i>P</i>	<i>M</i>	<i>C</i>								
Predrainage	0.167	0.049	0.118	0.075	0.058	0.017	30	17	47	25	57	32	46	26
Drainage	0.125	0.095	0.030	0.244	0.092	0.152	82	22	155	42	123	33	12	3
Modern	0.083	0.078	0.005	0.161	0.078	0.083	74	29	95	38	64	25	19	8

* Environmental predictability (*P*), contingency (*M*), and constancy (*C*) were calculated for years before Lake Okeechobee and the Everglades were diked and canals were built (Predrainage: 1916–1930), when drainage was full scale and uncontrolled (Drainage: 1931–1961), and when the Conservation Areas and Lake Okeechobee construction projects were completed and managed as a unit (Modern: 1962–1982).

higher water levels during Predrainage to lower lake levels during Drainage and Modern management periods.

When only three environmental states were specified in Colwell's analysis (Table 3), contingency values were similar to the model with four states but constancy (hence predictability) values changed. Because constancy increases with an unbalanced distribution of the number of observations in each state, collapsing the higher water level states increased constancy during Predrainage, when water levels were higher, but decreased constancy during Drainage and Modern periods with declining water levels. It is not clear which model is more appropriate: the three-state model may be more biologically correct, since it only requires a threshold level of water for successful kite nesting, but the four-state model recognizes the importance of water storage and flooding to present and future nest success. Nevertheless, it is clear from both models that water level predictability was low during Predrainage and that lowering the water table not only changed the patterns of predictability but increased the occurrence of poor and marginal states of water levels for kite nesting.

The impact of drainage operations on water levels is further illustrated by a significant decrease through

time of Lake Okeechobee mean, minimum, and maximum water levels (Table 4). Simultaneously, the annual range of lake levels was increasing as the annual minimum lake level decreased faster than the maximum. Increases in water level variability (Table 4), occurring simultaneously with increases in the strength of the annual cycle (Fig. 5), indicate that the duration of wet conditions was being shortened by water management operations. Drainage operations increased the rate of change in water levels; although heavy rains in late summer often cause sharp increases in Lake Okeechobee water levels, especially in September, water could still be discharged more quickly as drainage capabilities via canals increased through this century.

Snail Kites may use water levels as a proximate cue, along with snail density and other environmental cues, to determine when and where to reproduce. Once nesting has begun, a pair commits itself to 4 mo of reproductive investment, the outcome of which is dependent on the persistence of suitable water levels. Changes through time in the reliability of water level as a cue were examined by comparing fourth-order autocorrelations (the correlation between water levels 4 mo apart). Correlations between present water levels and those 4 mo in the future decreased significantly (one-sided test for equality of correlation coefficients: Rao 1952:232–

TABLE 4. Analyses of variance comparing yearly minimum, mean, maximum, and range of water levels (in metres above mean sea level) at Lake Okeechobee during three water management regimes. Data are $\bar{X} \pm SD$. For a given yearly measure for which the *P* value is significant, management periods with the same superscript letters are not significantly different from each other (Fisher's LSD).

Yearly	Water management era:			<i>P</i>
	Predrainage (<i>N</i> = 15 yr) (1916–1930)	Drainage (<i>N</i> = 31 yr) (1931–1961)	Modern (<i>N</i> = 21 yr) (1962–1982)	
Minimum	4.19 ± 0.12	3.86 ± 0.58 ^A	3.72 ± 0.09 ^A	.002
Mean	4.54 ± 0.40	4.27 ± 0.29 ^A	4.22 ± 0.34 ^A	.013
Maximum	5.07 ± 0.10	4.77 ± 0.07 ^A	4.71 ± 0.08 ^A	.015
Range	0.87 ± 0.11	0.91 ± 0.06	1.00 ± 0.08	.058

233) from 0.553 in Predrainage to 0.389 ($z = 2.28$, $P = .011$) during Drainage, and to 0.406 ($z = 1.93$, $P = .26$) during the Modern period.

DISCUSSION

Several attributes of Snail Kite demography are important to consider in relation to the unusual ambisexual mate desertion system exhibited by this species (Beissinger and Snyder 1987). First, kite nest success (32%) is much lower than 12 other subtropical/tropical raptors that successfully fledged young from 65.5% of their nests, and 24 temperate raptors with an average success rate of 67.4% (from Newton 1979: Table 23). Overall, raptors have high nest success rates compared to other birds; however, nest success of Florida Snail Kites was lower than most passerines and water birds (Ricklefs 1969). Second, kites are capable of nesting at 1 yr of age while still in subadult plumage. This is much earlier than most other raptors of similar size, which may not be capable of breeding until 2–3 yr of age (Newton 1979). Third, Snail Kites are highly iteroparous, capable of producing several broods a year during a nesting season which in wet years may last up to 10 mo. The nesting season is long enough to permit production of three or conceivably four broods a year if an individual was a consistent deserter (Beissinger and Snyder 1987). Finally, Snail Kite populations in Florida are highly unstable, declining or expanding by 50% during years when water levels are low or high, respectively.

Analyses of Lake Okeechobee water levels, which directly affected Snail Kite nesting success and population size, indicated that levels declined throughout this century, and periods of wet conditions became shortened by management operations (Table 4). These changes impacted both short-term (annual) and long-term (drought–flood) water cycles (Figs. 3–5): annual cycles became stronger (more variable water conditions), while drought–flood cycles became gradually shorter, moving from a 10 or more yr cycle in the early 1900's toward a 5-yr cycle in recent years. Generally, water levels in Florida are highly unpredictable (Table 3) and probably difficult for Snail Kites to use as a cue in determining how to allocate reproductive effort.

Changes in Lake Okeechobee water level cycles are due to two factors, environmental influences and water management operations. There is some evidence for a decline in rainfall in the Kissimmee River basin during the past 20 yr (Shih 1983; W. C. Huber, *personal communication*, S. Lin, *personal communication*), partly as a result of fewer tropical disturbances and hurricanes (Shih 1983), and perhaps even to a change in rainfall cycles from a 5-yr cycle before 1930 to a 6-yr cycle after 1930 (G. Shih, *personal communication*). Water management operations probably influenced lake levels most strongly after 1930 (Blake 1980), due to the increased ability to store and discharge water via dikes and canals.

Both long and short water level cycles may have important demographic effects on Snail Kites. Changes in the annual cycle probably would have the most direct impact on kite nesting success, because successful nesting depends on four consecutive months of favorable water conditions (deep enough to keep marshes flooded beneath nests sites, both to deter predators and support local snail populations). Because drought may be the most important source of adult mortality for Snail Kites in Florida, changes in the frequency and duration of the drought–flood cycle may directly influence adult survival and life expectancy.

Mate desertion by the Snail Kite is a novel type of mating system (Beissinger and Snyder 1987). For a behavior such as mate desertion to evolve via natural selection, it must confer greater advantages upon individuals following that strategy than they can achieve by any available alternative strategy. That is, desertion must be an ESS (Maynard Smith 1982). Because selection generally favors individuals that produce more reproductive offspring throughout a lifetime than their competitors, the most likely advantage of mate desertion should be in these terms relative to the fitness of individuals that either (1) remain and continue investing in the current brood (Maynard Smith 1977), or (2) do not desert but instead lay more eggs and raise more offspring.

Because mate desertion behavior probably confers higher fitness benefits to Snail Kite parents that desert and can potentially renest than those that tend offspring (Beissinger and Snyder 1987), the sexes should be in conflict over which one will desert at a given nest. Selection should favor the individual (or sex) that deserts first (Trivers 1972, Dawkins and Carlisle 1976, Maynard Smith 1977). This leads to a scenario of parents deserting earlier and earlier. Rather than be stuck tending the offspring alone for 3–5 wk (Beissinger and Snyder 1987), a parent might be willing to desert earlier than its mate, even at the cost of a partial reduction of the first brood, if there is a sizeable chance of obtaining another mate and renesting successfully (Maynard Smith 1977). But because Snail Kite nests fail at a high rate (>68%; Table 1), mostly before hatching (Fig. 1, Table 2), there is a low probability that deserters will be able to nest again successfully. It is probably maladaptive for a Snail Kite parent to desert so early that it sacrifices the survival potential of any of its first brood for a one-in-three (Table 1) chance of successfully rearing another brood. Kite desertion behavior suggests that parents desert after the young have reached the age at which they have virtually a 100% chance of surviving when tended by only one parent (Beissinger and Snyder 1987). Thus, it seems unlikely that mate desertion behavior in the Snail Kite evolved solely from a context of a clutch size that resulted from a conflict between the sexes over which one would desert earlier.

A possible scenario for the transition from biparental

care to the Snail Kite mate desertion system can be inferred from analysis of demographic traits and environmental regimes. The demographic characteristics of this kite population appear to be related to high environmental uncertainty and the changing environment of southern Florida. Early age of first reproduction, variable nesting season (Table 1), and high degree of iteroparity (multiple brooding) may be adaptations to high environmental uncertainty. Partly as a result of the highly unpredictable Florida water regime and its effects on snail populations, Snail Kite nest failure rates are high (Tables 1 and 2, Fig. 1) and populations are unstable. In this study, kites did not respond to increases in snail abundance by facultatively increasing clutch size (Fig. 2). Instead, kites responded behaviorally to changes in food abundance by deserting their mates in the midst of a breeding cycle and presumably attempting to remate and reneest (Beissinger and Snyder 1987). Below I discuss how the effects of environmental uncertainty on demographic traits might select for mate desertion in Snail Kites.

*Environmental uncertainty, clutch size,
and iteroparity*

Clutch size and parental care patterns may be considered coadapted traits or a strategy (*sensu* Stearns 1976). Males and females, however, may pursue different reproductive strategies to maximize fitness. In species with extended periods of parental care, it is often unclear whether (female) clutch size has become adjusted by a particular pattern of male parental care, or whether the pattern of male parental care is the result of selection for a particular (female) clutch size. The sex with the greater potential variance in reproductive success should determine whether clutch size has influenced parental care patterns or vice versa (Fisher 1930).

Environmental uncertainty may affect the potential for variance in reproductive success differently for males than for females. Potential responses by parents to environmental uncertainty was discussed by Low (1978); these include altering the timing of reproduction, the amount of reproductive effort (e.g., clutch size, egg size, parental effort), and the degree of iteroparity (e.g., asynchronous development and multiple brooding). Males can adjust the timing of reproduction but not clutch size or egg mass, which are controlled primarily by females (although courtship feeding can be an influence; Royama 1966, Nisbet 1973). Increasing polygyny by decreasing parental effort may be a viable option for males, but this may depend upon how much of their resources must be invested to secure copulations, and the source of offspring mortality. If parents can prevent offspring mortality by exerting more parental effort, and if males must make substantial investments to secure copulations (as in kites; Beissinger 1987), then male responses to uncertain environments may be limited to either increasing parental effort or mitigating

lost reproductive effort. However, females may respond to environmental uncertainty by adjusting the timing, amount of effort, and degree of iteroparity in reproduction, and also by mitigating costs. Thus, selection may act as strongly on females as on males, leading to equal and possibly higher variability in reproductive success among females than among males.

Iteroparous organisms may assess environmental quality to determine how much effort to invest in any reproductive bout. For instance, in some birds, females adjust clutch size in response to variation in food resources (Lack 1968, Klomp 1970). In fluctuating environments, organisms may have difficulty in estimating future environmental quality reliably. Individuals that underestimate environmental quality and lay smaller clutches would have a slightly lower fitness than individuals laying larger clutches. Individuals that overestimate environmental quality, however, may pay the cost of wasted reproductive effort (lost future fitness) and possibly the additional cost of decreased reproductive success (lower present fitness) due to brood reduction or nest failure (Bryant 1979, Slagsvold 1984, Røskaft 1985, Morris 1986). Therefore, in unpredictable environments individuals might be selected to hedge their bets by laying smaller clutches (Stearns 1976), especially if adult survivorship is high relative to that of dependent young (Low 1976, 1978, Goodman 1979).

A smaller clutch size might also allow females to lay replacement clutches more quickly. Compromises between clutch size and iteroparity should be common in parental organisms that have high rates of reproductive failure and long breeding seasons (compared to the development time of the young), selecting for smaller clutches (e.g., Ekman and Askenmo 1986) and a greater degree of multiple brooding. Alternatively, organisms with short breeding seasons and high reproductive success should channel more energy into a larger clutch size. The cause of reproductive failure will determine whether organisms should respond to environmental changes by altering clutch size or by being more iteroparous. If reproductive failure is caused mostly by factors unaffected by the degree of parental care, compromises between clutch size and iteroparity should strongly favor iteroparity (Low 1976, 1978, Stearns 1976).

*Clutch size, iteroparity, and mate
desertion in Snail Kites*

Snail Kites probably cannot accurately estimate trends in environmental quality at the beginning of a 4-mo nesting cycle because Everglades water level predictability is very low and appears to change through time. Water level variability is partly responsible for large year-to-year fluctuations in snail abundance (Kushlan 1975; S. R. Beissinger, *personal observation*) and kite nesting success. That Snail Kite clutch size in this study did not vary in relation to changes in snail

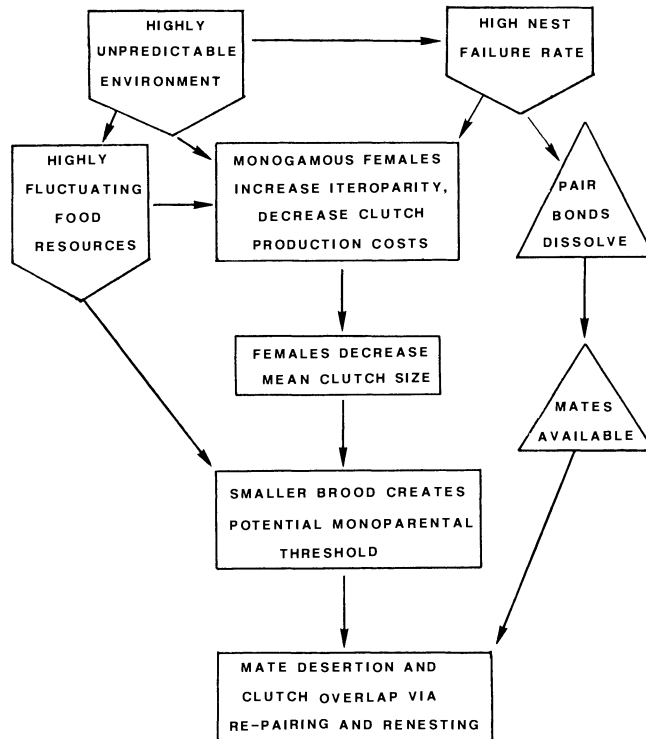


FIG. 6. A scenario for the transition from biparental care to mate desertion. Starting with an organism where both parents care for the young, selection acts on female reproductive behaviors via forces in the physical (pentagles) and social (triangles) environment. An unpredictable environment, fluctuating food resources, and a high nest failure rate cause females to become more iteroparous. As a result of selection for a smaller average clutch size, one parent can desert its mate when monoparental care is as effective as biparental care (monoparental threshold). Potential mates for remating may be secured from other pairs that have failed. A long breeding season allows re-pairing and re-nesting, resulting in clutch overlap.

abundance suggests either the cost to females of over-investment in clutches is high, or environmental predictability is so low that favorable conditions may change quickly.

Low nesting success, mostly due to factors unaffected by parental care (Table 2), and high environmental uncertainty would select for female kites that hedged their bets by laying fewer eggs, even though a modest reduction in clutch size results. Female Snail Kites cut costs in egg production by receiving the majority of food from their mates during courtship while expending little energy themselves, which results in males investing more reproductive effort than females do in egg-laying (Beissinger 1987). Having invested less effort in a bout, females that lay smaller clutches may be able to lay replacement clutches more quickly after nest failure than females that invested heavily in larger clutches (e.g., Smith and Roff 1980, Slagsvold 1984). In an unpredictable water regime, more nests of fewer young increase the probability of completing at least one successful nesting attempt because each nest has an independent probability of survival (Low 1978).

Therefore, mate desertion in Snail Kites may have evolved in response to a small average clutch size (Fig. 6). During conditions of low snail abundance, biparen-

tal care may be required throughout the nesting cycle to provide enough snails to fledge all nestlings; however, under conditions of high snail abundance, a single parent alone may be sufficient to feed all of the young, allowing one parent to desert at the proper time with little or no loss of fitness (Beissinger and Snyder 1987). Deserters may then have the opportunity to find a new mate and re-nest if environmental conditions permit. Because the nest failure rate is high and the nesting season is long, potential mates may be relatively easy for Snail Kite deserters to secure when other pair bonds begin to dissolve after nest failure (Fig. 6). Rather than gamble by increasing clutch size under temporarily but unpredictably favorable environmental conditions, Florida Snail Kites may increase fitness by deserting at the appropriate time and overlapping clutches.

Clutch overlap occurs when individuals divide their reproductive effort between successive clutches (Burley 1980, Hill 1986, Westmoreland et al. 1986). Burley proposed clutch overlap as a reproductive tactic alternative to varying clutch size that monogamous species may use if there are large differences in the amounts of energy required to rear offspring through various stages of development (i.e., a critical period in offspring development) or when only a few offspring can be raised

TABLE 5. Snail Kite clutch size in Florida by era. All data were from museum collections except those from 1979–1983, which were gathered during this study (Fig. 2). Clutch size of one ($N = 6$) was excluded as these clutches probably were never completed.

Era	No. clutches	Snail Kite clutch size										Mean size
		2		3		4		5		6		
		No.	%	No.	%	No.	%	No.	%	No.	%	
1880–1925	91	12	13	54	59	17	19	8	9	0	0	3.23
1925–1959	57	9	16	43	75	4	7	0	0	1	2	2.96
1979–1983	156	48	31	105	67	3	2	0	0	0	0	2.71

because of increasing cost functions for additional young.

Clutch overlap in Florida Snail Kites is different from the system that Burley (1980) observed in Rock Doves (*Columba livia*). In doves, both members of a pair overlap clutches by initiating a new nesting cycle together, thus increasing the fitness of both mates. A variation of this strategy, termed “double clutching” (Graul et al. 1977), is exemplified by the Mountain Plover (*Charadrius montanus*); clutch overlap occurs when the female produces a second clutch, fathered by the same male, and assumes all parental duties herself while the male tends the first clutch (Graul 1973). Unlike these species, clutch overlap in Snail Kites offers asymmetrical benefits that could cause conflict between mates over which will desert (Beissinger and Snyder 1987). Deserters increase their fitness by leaving the young in the care of their mate and may attempt to overlap clutches by renesting with another mate (bigamy), but nest tenders probably lose fitness because they are unable to overlap clutches, having been forced to assume all the investment remaining for brood rearing (e.g., Trivers’ cruel bind, 1972). Thus, a deserting Snail Kite does not overlap clutches by investing simultaneously in two clutches, but by forcing its mate to invest enough for both of them while the deserter renests.

There are several reasons why Snail Kite deserters usually overlap clutches by finding a new mate rather than remaining with their former mate as some other birds do (Lack 1968, Oring 1982). First, individual kites that do not desert risk being deserted by their mates, an outcome that would be strongly selected against (Trivers 1972, Dawkins and Carlisle 1976). Second, individuals that simply waited and mated again with their former mate would forfeit 3–5 wk (one-quarter of a nesting cycle) which could be used to begin a new nesting attempt (Beissinger and Snyder 1987). Third, because Snail Kite males perform nearly all of the nest-building duties and provision females for egg-laying (Beissinger 1987), they are probably unable to expend the large amounts of prezygotic effort required for a new nesting cycle while simultaneously caring for offspring. Attempts to overlap clutches while caring for the young occurred at only 2 of the 28 deserted nests in this study; both overlappers were males, one attempting to secure a new female, and one remating

with its present mate (Beissinger 1984). Both males abandoned their efforts to feed their mates within a week and reverted to caring for the young.

In summary, compared to altering clutch size, overlapping clutches affords a high degree of flexibility in assessing and responding to environmental conditions, since no extra investment is necessary unless immediate environmental conditions are favorable. Wasted reproductive investment can be minimized. Deserters may even save a significant portion of the reproductive effort required in a bout by deserting (Beissinger 1984).

Kite clutch size decline

If selection favored a smaller average clutch size and increased iteroparity in female kites, clutch size may have declined from larger clutches of perhaps four, five, or six eggs to the present sizes of two, usually three, and very rarely four eggs (Fig. 2). Based on evidence from museum collections and recent field studies, it appears that the clutch size of Snail Kites in Florida may have declined during the past 60 yr (Table 5). More than one-quarter of the clutches collected before 1925 contained four or more eggs (“large clutches”). Large clutches declined in frequency to 9% during the mid-1900’s and comprised only 2% of clutches observed during my field studies. Concurrently, the frequency of two-egg clutches increased from 13% before 1925 to 16% in the mid-1900’s to 31% in recent studies. The distribution of clutch sizes (two, three, or \geq four eggs) differed significantly among eras in Florida ($\chi^2 = 45.6$, $df = 4$, $P < .001$); the distribution of pre-1925 clutches differed significantly from midcentury ($\chi^2 = 7.6$, $df = 2$, $P = .023$) and modern clutches ($\chi^2 = 41.0$, $df = 2$, $P < .001$), and the distribution of midcentury clutches differed significantly from modern clutches ($\chi^2 = 9.11$, $df = 2$, $P = .01$).

Oologists were known to collect unusual or large clutches for novelty or financial rewards, and this could account for the apparent decline in kite clutch size through this century. However, since kite clutches were rather rare in collections and hard to obtain due to the difficulties of collecting deep in the Everglades (Nicholson 1926), it seems unlikely that collectors would pass over smaller clutches to collect larger ones, especially since these eggs brought a very good price (e.g., \$32.50 per egg in 1922, much more expensive than those of most raptors or passerines; Barnes 1922). Also, collec-

tors could have biased collections towards smaller clutches by collecting clutches before egg-laying had been completed. In any event, it is possible that there has been a historical decline in kite clutch size.

Apparent changes in Snail Kite clutch size during this century parallel changes in environmental quality in the Everglades (Parker et al. 1955, Tebeau 1971, Blake 1980). Originally more than one-fourth of the Florida peninsula was covered with surface water much of the year. Drainage in the peninsula had begun by the early 1900's (see Methods). Minimal effort was made to control freshwater runoff from the Everglades through the major canals that emptied into the Atlantic Ocean. The Everglades became dry much of the time and fires were commonplace. The water table probably has been permanently lowered by as much as 1.5 to 2.1 m in some places. Also, year-to-year variation in water levels increased, annual cycles changed, and water levels became a less predictive cue for favorable nesting conditions (see Fig. 5, Tables 3 and 4).

Irresponsible drainage may have led to massive kite nest failure, lack of snails, and adult starvation, causing populations to decline from the late 1920's to the early 1970's. Evidence from the early 1900's indicates that kites were abundant (Nicholson 1926, Howell 1932, Bent 1937), undoubtedly numbering in the thousands. By the 1940's and 1950's, numbers had declined, possibly to as low as 50–100 birds (Sprunt 1945, 1954), and by the mid-1960's perhaps to as few as 25 (Stieglitz and Thompson 1967, W. Dineen, *personal communication*) and no more than 50 or 60 existed (Sykes 1979).

In a small population of kites, any slightly adaptive behavior could cause large selective advantages and spread through a population quickly (the Founder principle; Mayr 1963). Thus, a decrease in kite clutch size could occur over a 60-yr period of directional selection and declining kite numbers.

Nevertheless, Everglades environmental predictability was probably low enough before drainage began (Fig. 5, Table 3) that selection for a smaller clutch size could have already been occurring before drainage operations increased the magnitude of selection via environmental degradation. However, if changes caused by human intervention through water management are partly responsible for poor environmental quality in Florida, a small average clutch size, multiple brooding, and mate desertion could be found in Florida kites but not in Central or South American populations (Amadon 1975). Present studies are focusing on mate desertion in these populations.

Ambisexual mate desertion

Several key factors may have selected for mate desertion leading to polygamy in Snail Kites (Fig. 6): (1) a clutch size that, if limited by food, is selected more towards the years of low snail abundance than years of high abundance. Selection for a smaller average clutch

size may be a result of high environmental uncertainty, high variability in food abundance from year to year, and a high nest failure rate; (2) the opportunity for multiple brooding due to a potentially long breeding season and a high availability of mates due to frequent nest failure; and (3) significant amounts of time and energy that can be saved by deserting. Mate desertion in Snail Kites occurs as a facultative response to a small average clutch size under conditions of high snail abundance.

The pathway proposed in this paper to account for the evolution of mate desertion in Snail Kites is similar to that proposed to explain the evolution of avian polyandry (Jenni 1974, Erckmann 1983, Oring 1986). Both models are based on small average clutch sizes that do not vary with changes in food resource levels, high nest failure rates, and the opportunity for multiple clutching. Ambisexual mate desertion in the Snail Kite may be viewed as an intermediate step in the continuum of mating systems between monogamy and classical polyandry (Oring 1986). The prime difference, of course, is that either Snail Kite parent may desert to take advantage of the opportunity for multiple brooding. Theoretically, the sex of the deserting parent depends on the costs and benefits of desertion to each mate (Boucher 1977, Maynard Smith 1977, Alexander and Borgia 1979). The unique pattern of mate desertion by either sex in Snail Kites, however, could be an effect of the timing of mate desertion.

When mate desertion occurs late in the nesting cycle, the only viable option for the deserted Snail Kite parent is to remain and care for the young, because the probability of renesting successfully is low while that of successfully raising the current brood is high (Trivers 1972, Maynard Smith 1977, Beissinger and Snyder 1987). Ambisexual mate desertion might be expected to occur when (1) desertion happens relatively late in a reproductive bout, (2) the operational sex ratio (Emlen and Oring 1977), hence the opportunity to remate, is variable, (3) parental duties are shared throughout a reproductive bout such that either sex is equally capable of rearing the young alone, and (4) the costs of establishing a new nest site or territory are minimal (Beissinger and Snyder 1987). High variation between pairs in the partitioning of parental care duties between mates (Beissinger 1984) may be a characteristic of ambisexual mate desertion systems, since mate assessment prior to desertion is likely, mates may be in conflict over the opportunity to desert, and each of the parents should be equally capable of performing parental duties.

Ambisexual mate desertion leading to polygamy might occur in other organisms with highly developed parental care that is executed equally well by either sex. This eliminates most mammals, because during gestation females alone care for the young, and at birth young are dependent on milk provided by females for extended periods, allowing males the opportunity to

desert. Birds are the most likely vertebrates to exhibit ambisexual mate desertion, since the parental duties throughout a reproductive bout can be performed by either sex, and reproductive investment often appears to be shared equally (Lack 1968, Pierotti 1981, Oring 1982). Of the other vertebrates, only a few species of fish provide extensive parental care (Ridley 1978) but ambisexual mate desertion has yet to be reported (Blumer 1979, Perrone and Zaret 1979).

Tropical birds may be most likely to have smaller average clutch sizes, permitting mate desertion, because they have long breeding seasons (allowing multiple brooding) and are subject to high nest failure rates, due to predation or environmental changes (Skutch 1966). For instance, selection for a small clutch size and iteroparity may in part explain the evolution of clutch size and male mate desertion in the White-bearded Manakin (*Manacus manacus*; Lill 1974). However, owing to the difficulties in detecting desertion late in a reproductive cycle, ambisexual mate desertion may be easily overlooked in other vertebrates where both parents appear to care for the young.

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