REPRODUCTION AND DEMOGRAPHY OF THE FLORIDA EVERGLADE (SNAIL) KITE[1]

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Abstract. An 18-year study of reproduction and survival of the Florida Everglade (Snail) Kite (*Rostrhamus sociabilis plumbeus*) has revealed the following: extremely poor nesting success (only 13.6% of nests found at the nest-building stage successful); extremely long breeding seasons (some reproductive activity in almost all months in good years); frequent multiple brooding and frequent renesting after failure; low egg hatchability (81%); high failure rates due to nest collapse, desertion, and predation; extremely high survival of juveniles and adults under good water conditions; and high vulnerability to drought due to near total dependency on a single species of drought-sensitive snail for food. Despite low nesting success, the species has increased rapidly under good conditions, mainly because of multiple nesting attempts within long breeding seasons and high survival rates of free-flying birds.

Nesting success varied significantly between regions and nest substrates, but not as a function of seasons or solitary vs. colonial nesting. While nesting success was reduced in low water years, this effect was at least partly due to heavy use of poor nest substrates under such conditions. Clutch size and numbers of young per successful nest varied with regions, but not as a function of seasons or water levels. The effects of coloniality on clutch size and numbers of young were inconsistent. Significant effects of nest-substrate types on clutch size and numbers of young were apparently artifacts of substrate differences between regions.

Key words: Florida Everglade Kite; Snail Kite; Rostrhamus sociabilis; *demography; endangered species.*

INTRODUCTION

From the mid-1960s to the present, the nesting biology of the endangered Florida Everglade (Snail) Kite (*Rostrhamus sociabilis plumbeus*) has received considerable study (e.g., Stieglitz and Thompson 1967; Chandler and Anderson 1974; Sykes 1979, 1987a, 1987b; Snyder et al. 1984; Beissinger 1986, 1987a, 1987b, 1988; Beissinger and Snyder 1987). During this period the wild population increased from several dozen birds to a total averaging about 400–500 individuals (Sykes 1979, 1983a; Rodgers et al. 1988; Fig. 1). Between 1966 and 1983 we monitored 666 Everglade Kite nesting attempts and made intensive banding and telemetry studies. Here we present detailed analyses of nesting success and survival

derived from these studies, and characterize the unusual and complex demography of the species.

METHODS

Field studies were conducted in south-central Florida, primarily on Lake Okeechobee (Glades, Hendry, and Okeechobee counties) and in State Water Conservation Area 3A (CA3A) of Dade and Broward counties, but also to a lesser extent on Lakes Kissimmee and Tohopekaliga (Osceola County). For a description of these areas and their use by kites see Beissinger and Takekawa (1983), Beissinger and Snyder (1987), and Sykes (1983b, 1984). Studies from 1966 through 1977 were conducted by REC; those of 1978 through 1980 by NFRS, REC, and SRB; and those of 1981 through 1983 by SRB.

In Table 1 we present summary data on the geographical-seasonal distribution of nesting attempts studied and the seasonal distribution of field observations. Our investigations had wide
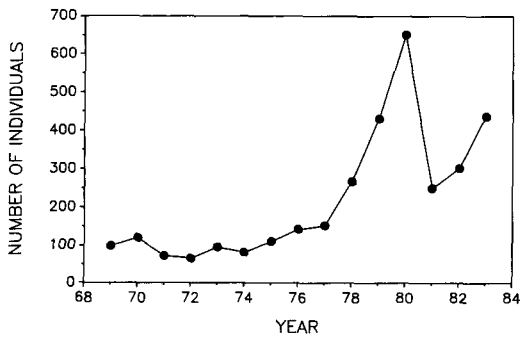
FIGURE 1. Population trends for the Florida Everglade Kite (1969–1983). Data for 1969–1980 from Sykes (1979, 1983a), for 1981 from Beissinger (1984), and for 1982–1983 from Rodgers et al. (1988).

enough seasonal durations from 1970 through 1982 to allow reasonably comprehensive determinations of the bounds of full breeding seasons. Because we documented no nest initiations in September and October, the potential breeding season for each year was considered to start in October of the previous year and run through September of the year in question. The totals given do not include all nesting attempts of the

population during the study period, as not all nesting areas were covered in all years and some nests were surely missed in every year, even in the nesting areas studied intensively.

Nests were visited at irregular intervals, generally several times a month. During early nesting stages, visits were generally limited to quick inspections (direct or by a mirror-pole) of nest contents. However, visits involving processing of young sometimes took a half hour or longer.

From 1978 through 1983 we banded 351 young and nine adults with unique color-band combinations or numbered PVC bands in addition to lock-on USFWS aluminum bands. These banded birds supplemented 65 young that had been color- and aluminum-banded from 1968 to 1977 by Sykes (1979). All birds banded in our studies were also measured (weight, wing length [chord], and culmen).

At 12 nests, repeated measurements of young were taken to develop standards for aging young of unknown hatching date. Both weight and culmen length showed curvilinear and variable relationships with age, approaching asymptotes before fledging (Beissinger 1984). Wing length

TABLE 1. Numbers and geographical/seasonal distribution of Everglade Kite nesting attempts studied 1966–1983, and number of broods possible for deserters and nondeserters.

Year	No. of documented nesting attempts[a]				Inclusive dates and (no. of weeks) for nest initiations[b]		No. of successful broods possible[c]		Months of field observation[d]
	CA3A	Okee	Kiss	Toho			ND	D	
1966[e]		3			10 Feb to 17 Jun	(18.1)	2	2	Apr to Jul
1967[e]		1			—		—	—	Apr to Sep
1968[e]		1			4 Mar		—	—	Oct to Dec, Mar to Jun
1969[e]		1			1 Nov		—	—	Nov, Apr to May
1970		2			29 Mar to 17 Apr	(2.9)	1	1	Oct to Sep
1971		5			1 Feb to 12 Apr	(10.1)	1	2	Oct to Jul
1972		5			28 Feb to 5 May	(9.7)	1	1	Oct to Jan, Apr to Sep
1973		28			5 Dec to 2 Jun	(25.7)	2	3	Oct to Jul
1974		23			24 Dec to 6 Apr	(14.8)	1	2	Nov to Jun
1975		30			4 Nov to 1 May	(21.1)	2	3	Nov, Feb to Sep
1976		29			10 Jan to 1 Jun	(20.6)	2	3	Oct, Nov, Jan to Sep
1977		45			18 Dec to 8 Jun	(24.7)	2	3	Oct to Sep
1978	120	16			25 Dec to 3 Aug	(31.7)	2	4	Oct, Nov, Jan to Sep
1979	120	49			13 Nov to 18 Jun	(31.1)	2	4	Oct to Sep
1980	20	5			25 Dec to 15 Jul	(29.1)	2	3	all except Jan, Mar, Jun, Sep
1981	8	12			3 Mar to 11 Apr	(5.7)	1	1	Jan to Jul
1982	1		17	38	1 Feb to 1 Jul	(21.6)	2	3	Dec to Aug
1983[e]	71	6	10		21 Jan to 12 Jun	(20.4)	2	3	Mar to Jun
Totals	340	261	27	38					

[a] Full names of nesting areas are Conservation Area 3A, Lake Okeechobee, Lake Kissimmee, Lake Tohopekaliga.
[b] Nests initiated in November and December included in totals for the following calendar year, as they clearly were part of that breeding season. No initiations documented for September or October.
[c] Assuming 16 weeks per brood for nondeserters and 10 weeks per brood for deserters; ND = nondeserters, D = deserters.
[d] All months in which at least one field survey was made are listed.
[e] Field coverage not extensive enough to give good grasp of full extent of breeding season.

increased more linearly with age and was still increasing steeply at fledging, providing the best measurement for aging birds. By dividing wing length development into two visibly distinct periods, separate regressions were fit to the data that accurately aged nestlings: (1) for chicks with wing length less than 40 mm, Age (in days) = $0.319 \times$ wing length in mm $- 4.289$ ($r^2 = 0.902$, SE $= 0.655$, $P < 0.001$), and (2) for chicks of more than 40-mm wing length, Age (in days) = $0.097 \times$ wing length $+ 4.069$ ($r^2 = 0.972$, SE $= 1.024$, $P < 0.001$).

Nests were back-dated to initiation dates, assuming the following time periods for nesting stages: nest-building period of 10 days; eggs laid at 2-day intervals; incubation starting with the first or second egg; incubation period of 27 days; nestling period of 30 days; postfledging dependency period of 6 weeks; total nesting cycle of 16 weeks (Beissinger 1984, 1987a, 1987b; Beissinger and Snyder 1987). In actuality, nest building was quite variable in length, ranging from less than a week to over a month. Although we do not have enough data to calculate an accurate mean length to nest building (one is rarely present for the very start of this activity), we have used 10 days as our best rough estimate. The length of the nestling stage was also somewhat variable, with young occasionally leaving the nest as early as 24–25 days or as late as 34–35 days from hatching. When no more information was available, midpoints of breeding stages were assumed in dating nests.

Clutch size was assigned only to nests that had clearly passed beyond the egg-laying period. The egg stage started with the laying of the first egg; the nestling stage with the hatching of the first egg.

To analyze egg hatchability we used only those nests for which clutch size was ascertained and which were followed to a stage when eggs should have hatched. For nests which had fewer young than eggs, it was often impossible to determine if the missing eggs had hatched and young had died and been removed, or if nonhatching eggs had been removed. In these cases we calculated minimum and maximum numbers of hatching eggs.

Nests were ranked as solitary or as colonial with (1) kites only, (2) waterbirds only (herons, ibis, or anhingas), or (3) kites and waterbirds. To qualify as colonial a given kite nest had to be within 100 m of at least one active nest of each of the particular associates in question.

Nests were classified by starting date for seasonal analyses. Early nests were started from November through February. During this season, cold fronts were frequent and winds were strong, making foraging difficult and posing threats to nest integrity. Mid-season nests were begun in March and April, a time of warming weather and usually falling water levels. Late nests started from May through August, the hottest and rainiest season.

In previous analyses Beissinger (1986) and Beissinger and Snyder (1987) presented nesting success figures for 1978 through 1983 based on all nests found before or at hatching of eggs. Here we refine and expand these calculations to compare success of nests found (1) before eggs were laid (the most valid measure of nesting success, but one which sometimes suffered from small sample size), (2) during the egg stage, and (3) before hatching (a measure including both of the previous categories and some additional nests for which the stage at finding was unclear, but was either nest building or incubation). As before, all nesting attempts involving at least some nest building are included.

We did not employ the Mayfield method (Mayfield 1961, 1975; Hensler and Nichols 1981) to estimate overall nesting success. This method entails calculations of survival probabilities for various discrete periods of the nesting cycle and could be applied successfully to our data for the egg stage and, to a lesser extent, the nestling stage because these periods varied relatively little in duration. Unfortunately, nest building varied greatly in duration and would provide problems in calculations. Ignoring this period in the analyses would be ill-advised because more than one-third of the nests found during nest building failed before eggs were laid. A high failure rate before egg laying was observed in all nesting regions.

Of particular importance is our treatment of the considerable number of nests (94) manipulated structurally. These nests were found tipping over and in imminent danger of collapse. Because of the endangered status of the kite, we generally transferred such nests to specially-built baskets mounted on poles in or very close to the original positions of the nests, although in nine cases we improvised other kinds of supports. The success rate of the manipulated nests was much higher than average, so inclusion of these nests at face value in calculations of nest success, as was done by Sykes (1979, 1987b), would greatly bias success upward from true natural nest suc-

cess. On the other hand, exclusion of these nests, as we did in earlier studies (Beissinger 1986, Beissinger and Snyder 1987), still biases success upward because the manipulated nests were not a random sample in potential for success (all were nests with virtually no chance for natural success). Thus, we now believe that the most realistic estimate of natural nesting success is not obtained by excluding these nests, but by including them all as nesting failures. Most of these nests were found in 1973–1978 and 1981–1982, and most were in cattails (*Typha* sp.). Even the sturdiest cattail sites (which we did not manipulate) had a very low success rate.

We considered nests to be successful if any young reached banding age (mid–late development). This presumably biased nest success upwards to a small extent since young were occasionally lost after this point (Beissinger 1986, Beissinger and Snyder 1987). The choice of the mid–late nestling stage as the endpoint of reproduction was made primarily because relatively few nests were followed beyond this stage (except for the years before 1978). When we documented losses of young subsequent to the mid–late nestling stage, the losses were included in calculations. Nests of unknown outcome were excluded from calculations. As there were few of these and most were nests visited only once, with no opportunity for revisitation, exclusion of these nests did not introduce appreciable bias.

Differences between the numbers of nests analyzed in this study and the numbers in earlier studies (Beissinger 1986, Beissinger and Snyder 1987) result from improvements in methodology incorporated in the present study.

The causes of nesting failure were rarely determined with certainty. A majority of failed nests were found empty and undisrupted, with no clear indications of why their contents were missing. Nevertheless, to gain some understanding from the data, we used the following classification scheme. We emphasize that it should be viewed as only a rough categorization of the causes of failure: (1) Apparent structural collapse—solitary or kite colony nests found collapsed, frequently following strong winds, within the time frame that they should have been active; also nests in kite-waterbird colonies that clearly collapsed when active, and all manipulated nests; (2) Probable structural collapse, possible desertion or predation—nests fallen or that were totally destroyed in kite-waterbird colonies (where collapse could also plausibly have been due to stealing of nesting material and nest disruption by the waterbirds, especially subsequent to failure for other reasons); (3) Apparent predation—nests where predation was directly observed or obvious signs of predator presence and nest disruption were found; also nests found empty within 2 days of previous observation of healthy chicks or eggs; (4) Probable predation, possible desertion, and scavenging—nests previously observed with healthy chicks or eggs found empty three or more days after previous checks; (5) Apparent desertion—nests never finished or found abandoned with eggs or live young in the nest; also desertion observed directly; (6) Probable desertion, possible predation, or disease—uneaten dead young found on the nest with other contents as well as the nest found intact; also nests in early stages that failed after severe weather or with no evidence that eggs were ever laid; (7) Probable human disturbance—nests in locations with signs of human activity (e.g., airboat damage to vegetation); and (8) Completely unknown—nests not monitored closely enough to determine anything about causes of failure.

Analyses would greatly underestimate the importance of nest collapse in the biology of the species if manipulated nests were not ranked as failures due to nest collapse, even though many of these nests proved to be successful or failed ultimately from other causes.

Nesting success, clutch size, and number of young per successful nest were each analyzed in relation to differences in region, nest substrate, season, coloniality, and water levels, using two- and three-way contingency tables corrected for empty cells when necessary (Conover 1980). Because clutch sizes of one and four eggs were extremely rare, contingency comparisons were made using only two- and three-egg clutches. Calculations were made using SYSTAT. All univariate tests were performed separately on nests found during nest building and incubation. But, because results from the two stages yielded similar conclusions, we combined them into nests found before hatching for most presentations here. This process maximized sample sizes and abilities to detect significant differences.

In addition, multivariate analyses were conducted using log-linear models in SAS to examine how nesting success, clutch size, or number of young were simultaneously related to nesting substrate, season, coloniality, and water levels. Since lake habitats contained nests in both herbaceous and woody substrates, while virtually all

TABLE 2. Everglade Kite nesting success by area, year, and stage found.[a]

Year	Area	Found nest building		Found at egg stage		Found before hatching	
		No. nests	Percent success	No. nests	Percent success	No. nests	Percent success
1968	Lakes	—	—	1	100.0	1	100.0
1970	Lakes	1	0.0	1	100.0	2	50.0
1972	Lakes	—	—	3	33.3	3	33.3
1973	Lakes	10	30.0	18	22.2	28	25.0
1974	Lakes	8	0.0	13	0.0	22	0.0
1975	Lakes	3	0.0	15	0.0	19	0.0
1976	Lakes	9	0.0	18	0.0	27	0.0
1977	Lakes	26	0.0	13	15.4	41	4.8
1978	Lakes	11	9.9	4	0.0	15	6.7
	CA3A	41	34.1	55	45.5	96	40.6
1979	Lakes	22	18.2	12	33.3	36	22.2
	CA3A	22	18.2	66	57.6	89	47.2
1980	Lakes	—	—	2	0.0	2	0.0
1981	Lakes	12	0.0	—	—	12	0.0
	CA3A	2	0.0	5	0.0	7	0.0
1982	Lakes	39	2.6	12	8.3	51	3.9
	CA3A	1	0.0	—	—	1	0.0
1983	Lakes	3	0.0	6	16.7	9	11.1
	CA3A	26	19.2	12	33.3	38	23.7
Totals:[b]							
Overall		236	13.6	256	32.0	499	22.8
Lakes		144	6.7	118	12.7	268	9.0
CA3A		92	25.0	138	48.5	231	39.0
Lakes (1978–1983)		87	6.9	36	16.7	125	9.6

[a] Only nests found at nest-building and egg stages and followed to known outcomes were considered. All manipulated nests considered failures. Successful nests were those producing at least one young to banding age.
[b] Statistical comparisons of nesting success:

1. Lakes (all years) vs. CA3A

Nest building	$\chi^2 = 16.8$, df = 1, $P < 0.001$
Egg stage	$\chi^2 = 37.5$, df = 1, $P < 0.001$
Prehatching	$\chi^2 = 63.4$, df = 1, $P < 0.001$

2. Lakes (1978–1983) vs. CA3A

Nest building	$\chi^2 = 10.8$, df = 1, $P < 0.001$
Egg stage	$\chi^2 = 11.9$, df = 1, $P < 0.001$
Prehatching	$\chi^2 = 34.2$, df = 1, $P < 0.001$

nests in CA3A were built in woody substrates, separate log-linear models were constructed for CA3A (without a substrate term) and lakes (with a substrate term). Water levels were dropped from the log-linear models for clutch size and numbers of young in CA3A because sample sizes were too small during low water conditions. Statistical significance for all univariate and multivariate tests was set at $P < 0.05$, and high significance at $P < 0.01$.

RESULTS

OVERALL NESTING SUCCESS AND PRODUCTIVITY

Table 2 summarizes the success data for all analyzable nests. Only 13.6% of the nests found at the nest-building stage, 32.0% of the nests found at the egg stage, and 22.8% of all nests found before hatching produced young. Furthermore, the number of young produced per nest found at the nest-building stage averaged only 0.28. Even in the very best years for food supplies and water levels, and in the very best local regions, nesting success rose only to 34% for nests found at the nest-building stage.

Nesting success varied between areas of study (Table 2). Nests in the Everglades habitat of CA3A were three to four times as successful as those in lake habitats. This difference was highly significant, both for nests found in all years, and for comparisons limited to those years when both lakes and CA3A were monitored (1978–1983). Much of the difference can be attributed to the intensive use of cattails for nesting on the lakes, whereas only one CA3A nest was in cattails. As

TABLE 3. Factors affecting Everglade Kite nesting success.[a]

	Lakes			CA3A			All regions		
Comparison[b]	No. nests	Percent success	χ^2	No. nests	Percent success	χ^2	No. nests	Percent success	χ^2
Nest substrate:			21.9**			0.5			55.7**
Herbaceous	163	3.1		4	50.0		167	4.2	
Woody	68	22.1		220	39.1		288	35.1	
Season:			0.6			1.3			3.6
Early	94	10.6		76	43.4		170	25.3	
Middle	130	7.7		92	34.8		222	18.9	
Late	44	9.1		63	39.7		107	27.1	
Coloniality:			0.3			0.0			0.8
Solitary	57	12.3		84	39.3		141	28.4	
Colonial	154	9.7		147	38.7		301	23.9	
Form of coloniality:			2.0			3.3+			29.6**
Kites only	138	8.7		41	26.8		179	12.8	
Kites + waterbirds	15	20.0		104	43.3		119	40.3	
Water levels:			4.6*			5.3*			25.4**
Low	86	3.5		8	0.0		94	3.2	
High	182	11.5		223	40.4		405	27.4	
Present/past water levels:			5.8+			10.6**			31.5**
Low	86	3.5		8	0.0		94	3.2	
Lag one year	31	6.4		38	23.7		69	15.9	
High	151	12.6		185	44.8		336	29.8	

[a] Nests considered were found before hatching. Successful nests produced at least one young.
[b] Probability levels for comparisons were as follows: + = $P < 0.10$; * = $P < 0.05$; ** = $P < 0.01$.

discussed below, nest success in cattails was very low. However, CA3A was also superior to the lakes in overall nest success when comparisons were limited to nests in woody vegetation (Table 3; $\chi^2 = 6.6$, df = 1, $P = 0.01$).

NESTING SUCCESS IN VARIOUS SUBSTRATES

Nest substrates influenced nest success greatly. Two nest substrates accounted for nearly three-fourths of the nesting attempts: willows (*Salix caroliniana*) and cattails. Only 3% of the nests found before hatching in cattails ($n = 159$) were successful, while the corresponding rate for nests in willows ($n = 189$) was 35%. Further, probable or possible nest collapse accounted for 64% of 152 failures of identifiable cause in cattails, as compared with only 16% of the 107 failures of identifiable cause in willows, a highly significant difference ($\chi^2 = 25.7$, df = 1, $P < 0.001$). In addition, the 47% overall success rate of the 74 egg-stage cattail nests that were transferred to baskets was similar to the 44% success rate of egg-stage willow nests ($\chi^2 = 0.2$, df = 1, $P > 0.5$). These results strongly suggest that the low success of unmanipulated cattail nests was due to poor structural support rather than to other habitat deficiencies.

With the exception of 58 nests in pond apple (*Annona glabra*), sample sizes of nests in other woody substrates were generally too low to allow meaningful comparisons with nests in willows. Success of pond apple nests found before hatching (41%) was marginally, but not significantly, greater than that of willow nests (35%), an effect, if it is real, that might be attributable to the better-developed branch structure of pond apples.

Nests in nonwoody substrates other than cattails were rare, although we did find several nests in bulrush (*Scirpus californicus*), maidencane (*Panicum hemitomon*), and sawgrass (*Cladium jamaicensis*). Nests in sawgrass were substantial, well-anchored structures and were mostly successful; those in bulrush and cane were precarious and were uniform failures. A full presentation of details on nesting success in various substrates is available from the authors on request.

Nests in herbaceous vegetation were highly significantly less successful than those in woody vegetation (Table 3). Though there were few nests in herbaceous substrates in CA3A, differences in nest success between substrate categories were not just an artifact of regional differences in success. Nests in woody vegetation were highly significantly more successful than those in herba-

TABLE 4. Numbers of Everglade Kite nests initiated by month, area, and year.

Year	Area[a]	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
1966[b]	Okee					1			1	1			
1968[b]	Okee						1						
1969[b]	Okee		1										
1970	Okee						1	1					
1971	Okee					2	1	1					
1972	Okee					1	1		2				
1973	Okee			2	2	6	4	10	3	1			
1974	Okee			2	3	3	9	5					
1975	Okee		2	6		4	8	6	1				
1976	Okee				4	12	8	2	2	1			
1977	Okee			6	2	10	7	6	7	4			
1978	Okee				4	6	5	1					
	CA3A			3	11	15	20	13	8	19	24	1	
1979	Okee		4	1	8	4	7	14	5	3			
	CA3A		2	12	33	9	25	18	16	3			
1980[b]	Okee				1				2		1		
	CA3A			3	13	2			1		1		
1981	Okee						6	6					
	CA3A						6	2					
1982	CA3A					1							
	Toho					3	4	17	8	3	1		
	Kiss						7	1	1	2			
1983[b]	Okee					6							
	CA3A				9	13	26	8	3	7			
	Kiss						1	3	4				
Grand total			9	35	90	98	147	114	64	44	27	1	
Lakes total			7	17	24	58	70	73	36	15	2		
CA3A total			2	18	66	40	77	41	28	29	25	1	

[a] Abbreviations as in Table 1.
[b] Seasonal field coverage not extensive enough to give good estimate of seasonal nest distributions.

ceous vegetation when analyses were limited to lake habitats.

EFFECTS OF SEASONS, COLONIALITY, AND WATER LEVELS ON NEST SUCCESS

Some nesting activity was detected in all months of the year, though no nest initiations were found for September and October (Table 4). The minimum periods for nest initiations (Table 1) ranged from 2.9–10.1 weeks in years of low kite numbers or low water levels to 24.7–31.7 weeks in years of high kite numbers and high water levels. No significant differences were detected in success of nests found during the early, middle, and late portions of the breeding seasons, either on the lakes or in CA3A (Table 3).

Overall, 400 of 590 (67.8%) classifiable kite nests were in some sort of colonial association (213 colonial with other kites, 184 colonial with other kites and waterbirds, and three colonial with waterbirds only), indicating that kites were more likely to nest in groups than alone ($\chi^2 = 74.7$, df = 1, $P < 0.001$). There were no seasonal

($\chi^2 = 0.7$, df = 2, $P > 0.70$) or regional ($\chi^2 = 1.95$, df = 1, $P > 0.16$) differences in tendencies of kites to nest in grouped associations.

Similarly, there were no significant differences in success between solitary and colonial nests (all associations combined) in any region (Table 3). Nevertheless, there were differences in success by specific colonial association. Nests in kite-waterbird colonies were highly significantly more successful than nests in colonies composed only of kites when all nests were considered (this comparison does not quite reach significance when regions are tested separately). However, the success rates found for these social groupings were very similar to those predicted simply by examining ratios of herbaceous and woody nest substrates for the groupings (see Table 3). No kite-waterbird colonies were situated in herbaceous vegetation, while 53.2% of nests in kite-only colonies were built in herbaceous substrates. These data alone lead to predictions of 35.1 and 18.7% nest success, respectively, for nests found before hatching in kite-waterbird colonies and

TABLE 5. Clutch size and number of young per successful nest in Everglade Kites as a function of region, nest substrate, season, coloniality, and water levels.

Comparison[a]	Clutch size[b]						No. young per successful nest[c]				
	1	2	3	4	$\bar{x}$	χ^2	1	2	3	$\bar{x}$	χ^2
Region:						4.5*					7.5*
Lakes	0	37	95	2	2.74		9	29	19	2.18	
CA3A	2	47	68	1	2.58		46	81	28	1.88	
All combined	2	84	163	3	2.66		55	110	47	1.96	
Nest substrate:						5.0*					10.1**
Herbaceous	0	24	72	1	2.76		1	6	8	2.47	
Woody	2	51	79	2	2.60		47	96	34	1.93	
Season:						2.7					4.1
Early	2	26	60	0	2.66		25	43	24	1.99	
Middle	0	37	76	3	2.71		20	37	16	1.95	
Late	0	21	27	0	2.56		10	30	7	1.94	
Coloniality:						0.29					12.4**
Solitary	2	24	48	0	2.62		23	21	20	1.95	
Colonial	0	53	90	3	2.65		29	77	23	1.95	
Water levels:[d]						1.1					3.5
Low	0	12	32	0	2.73		1	3	1	2.00	
High	2	72	131	3	2.65		54	107	46	1.96	
Present/past water levels:[e]						1.5					3.8
Low	0	12	32	0	2.73		1	3	1	2.00	
Lag one year	0	13	19	1	2.64		6	25	8	2.05	
High	2	59	112	2	2.65		48	82	38	1.94	

[a] Probability levels for comparisons were as follows: $+ = P < 0.10$; $* = P < 0.05$; $** = P < 0.01$.
[b] Includes manipulated nests.
[c] Excludes manipulated nests.
[d] Low years were 1968, 1971, 1974, and 1981–1982; other years were high.
[e] Low years as above; lag years 1969, 1972, 1975, and 1983; other years were high years.

kite-only colonies. When these percentages were used as expected values, success by specific colonial association did not differ significantly from the values predicted ($\chi^2 = 2.4$, df = 1, $P > 0.10$). Thus, the strong differences in success by substrate type largely accounted for the differences in success by specific social grouping.

Nest success differed with water levels (Table 3). When only present water levels were considered, success was significantly reduced in years of low water (and presumably snails) for all nests and all regions. Further, since snail (*Pomacea paludosa*) populations take several years to recover from severe drought, we also analyzed the data to see if effects on nesting success could be detected in the years immediately following drought years (lag years). Significant or nearly significant effects were found for all nests and regions (Table 3).

However, much of the effect of water levels on nesting success, at least on the lakes, was due to a significant shift in nest substrates during drought. During low water years 84% of nests on the lakes were in herbaceous substrates as opposed to 64% in high water years ($\chi^2 = 10.6$, df

$= 1$, $P < 0.001$). And when nest success rates by substrate type were used to predict nest success under different water levels in this region, the observed nesting success did not differ significantly from that predicted ($\chi^2 = 1.3$, df = 1, $P = 0.25$). This comparison came closer to significance in CA3A ($\chi^2 = 3.3$, df = 1, $P < 0.10$). Thus, it is not clear to what extent water levels affected nest success independent of substrate effects. The number of nests was small under low water conditions, and the difficulties in distinguishing effects of water levels alone from substrate effects may trace mainly to sample size problems, especially in CA3A.

CLUTCH SIZE, HATCHABILITY OF EGGS, AND YOUNG PER SUCCESSFUL NEST

Clutches varied between one and four eggs, with those of one and four being very rare (1.2% of the total) and three being the most frequent (64.6% of the total). The overall average was 2.66 (Table 5).

Clutch size was not discernibly affected by widely varying water conditions (Table 5). The frequency of two- and three-egg clutches did not

differ significantly between years of low water and years of high water, even when the lag-year effects of drought were considered. Clutch size was also not clearly affected by seasons or coloniality, although for CA3A alone clutches tended to be larger in solitary than in colonial nests ($\chi^2 = 3.5$, df = 1, $P = 0.06$).

On the other hand, clutch size was significantly larger on the lakes than in CA3A, and in herbaceous as opposed to woody substrates. However, there were extremely few nests in herbaceous substrates in CA3A, and when only the lakes were considered, clutch size did not differ significantly between woody and herbaceous substrates ($\chi^2 = 0.01$, df = 1, $P > 0.90$). Thus, the difference in clutch size between substrate types was apparently an artifact of regional differences in clutch size. Full details on clutch size by year and region are available from the authors on request.

Besides possessing a relatively low–moderate clutch size, the Everglade Kite is characterized by poor hatchability of eggs. Of 497 eggs laid and incubated, a minimum of 369 (74.2%) and a maximum of 435 (87.5%) hatched, for a mean percent hatch of only 80.9%.

The number of young per successful nest (Table 5) varied in a manner similar to clutch size. It averaged 1.96 throughout the study and did not differ significantly between high and low water conditions. Neither was there a significant difference in numbers of young in years following a drought (lag years) vs. high water or low water years. Probably because of an effect of clutch size on number of young, the number of young per successful nest was significantly higher (1) on the lakes than in CA3A, and (2) in herbaceous as opposed to woody substrates. As with clutch size, the overall substrate effect on number of young was apparently an artifact of regional differences, as numbers of young did not differ by substrate on lakes alone ($\chi^2 = 1.2$, df = 2, $P > 0.5$). The number of young per successful nest also did not change with season. The overall distribution of numbers of young per successful nest did differ significantly between colonial and solitary nests, but the mean young per nest was identical. However, solitary nests produced more young than did colonial nests in CA3A ($\chi^2 = 9.5$, df = 2, $P < 0.01$), while the reverse occurred on the lakes ($\chi^2 = 8.4$, df = 2, $P < 0.02$). The meaning of these opposed regional differences is unclear.

UNIVARIATE VS. MULTIVARIATE ANALYSES

In almost all cases, contingency table analyses of nest success, clutch size, and numbers of young yielded significant effects for region and nest substrate, although it appeared that the effects of substrate on clutch size and numbers of young were artifacts of regional differences in clutch size. While nest success was also affected by water levels, this relationship was due, at least partly, to shifts in substrate use with different water levels. No consistent effects were detected for seasons and coloniality.

Results from the log-linear models were similar to the results of univariate analyses when region and substrate were taken into account. In the log-linear model for nesting success on the lakes, only substrate was a significant variable ($P = 0.02$). Neither season, coloniality, nor water levels produced significant main effects ($P > 0.15$), and the only second-order interaction of near significance was between coloniality and water levels ($P = 0.07$). Nesting success in CA3A was similarly unaffected by season, coloniality, or water levels, and no second-order interactions were significant. For clutch size, none of the main effects (substrate, season, coloniality, or water levels) or second-order interactions were significant for the lakes, but in the CA3A model coloniality decreased clutch size significantly ($P = 0.03$). Sample sizes of numbers of young were too small on the lakes to allow log-linear analyses. In CA3A the number of young was not significantly related to seasons, but was (as in univariate analyses) related to coloniality ($P < 0.01$), and the interaction between seasons and coloniality was also significant ($P < 0.01$).

CAUSES OF NESTING FAILURE

Of the causes of nesting failure (Table 6) apparent or probable nest collapse was perhaps the most important (36.7 to 43.6% of the total failures of assignable cause). Failures due to apparent, probable, and possible predation accounted for 4.5 to 23.4 to 45.5% of the assignable failures, while failures due to apparent, probable, and possible desertion accounted for 17.6 to 32.8 to 58.6% of the assignable failures. Thus, although there was a high degree of uncertainty as to whether many nests had failed from predation or desertion, it appears that desertion was relatively frequent, possibly more frequent than predation.

TABLE 6.   Causes of Everglade Kite nesting failure.[a]

Causes	Lakes		CA3A		All areas	
	No. cases	Percent assignable causes	No. cases	Percent assignable causes	No. cases	Percent assignable causes
Apparent structural collapse	120	51.5	18	12.6	138	36.7
Probable structural collapse, possible desertion/predation	0	0.0	26	18.2	26	6.9
Apparent predation	13	5.6	4	2.8	17	4.5
Probable predation, possible desertion	27	11.6	44	30.8	71	18.9
Apparent desertion	38	16.3	28	19.6	66	17.6
Probable desertion, possible predation	35	15.0	22	15.4	57	15.2
Probable human disturbance	0	0.0	1	0.7	1	0.3
Completely unknown	20	—	10	—	30	—
Totals	253		153		406	

[a] Includes all manipulated nests ranked as failures due to apparent structural collapse.

The ultimate causes of desertion were usually not determined. In many cases we suspected food stress. Some nests were deserted when the surrounding marshes dried up. Direct observations of others indicated that adults were having trouble finding food prior to desertion. Several times we saw abandonment of whole kite colonies following several days of cold weather in winter. Observations of foraging adults indicated that cold weather greatly depressed snail capture rates (Carey 1985, pers. observ.). Other pairs deserting during nest building apparently gave up because the nest sites were too poor to sustain continued nest building. Still other desertions were quite clearly due to nonhatching eggs.

Positive evidence for specific predators destroying nests was limited, very likely because many reptilian and avian predators do not normally disrupt nests or leave clues as to their activities. However, we found Everglade rat snakes (*Elaphe obsoleta rossalleni*) coiled up in three previously active nests, and in another we found a cottonmouth moccasin (*Agkistrodon piscivorous*) with the right number of body bumps to match clutch size. Another nest in relatively shallow water contained chewed remains of young kites, raccoon (*Procyon lotor*) fur, and raccoon fecal material. We doubt that raccoons are normally a significant threat; kites usually nest over deep water and raccoons limit their foraging largely to the shoreline. We also found a few nests with punctured eggs, possibly resulting from activities of Boat-tailed Grackles (*Quiscalus major*). We directly witnessed one apparent case of egg predation by this species, but on other occasions we monitored the fates of deserted kite

eggs in areas of grackle abundance, and the eggs were left untouched over periods of weeks.

In addition, we once flushed a Turkey Vulture (*Cathartes aura*) from a kite nest that had contained healthy nestlings a few days earlier. Fresh blood on kite bones in the nest suggested predation rather than scavenging of dead nestlings. We also found several nests that were apparently overwhelmed by ants (*Crematogaster* sp.), causing desertion during the egg stage and loss of young in the nestling stage. Snyder et al. (1984) noted attacks by larval *Dermestes nidum* on kite nestlings in 1978 and 1979, resulting in failure of one nest. No dermestid attacks had been seen in earlier years. Dermestids continued to attack kite nestlings from 1980 to 1983 (15% of the 40 nests in which young were examined; one probable nest failure), although this still appears to be a low-level threat.

MULTIPLICITY OF NESTING ATTEMPTS

The kite breeding season in Florida is often long (Tables 1, 4), with nest initiations spanning 6–7 months in good years. The length and shape of the nest-initiation curve in certain years (e.g., 1978 and 1979), with peaks spaced about 3–4 months apart, suggested widespread multiple brooding. By resightings of banded birds and birds clearly recognizable by plumage idiosyncrasies, we confirmed multiple nesting efforts within years in nine cases, a substantial total considering the paucity of banded birds until the latter years of the study. Seven of the nine cases were successful nestings followed by second attempts (three of them successful), while two cases were renesting attempts after failures (both unsuccessful). In

1982 a telemetered female made three nesting attempts with at least two different males: the first nest was abandoned before egg laying; the second fledged young which she deserted, leaving her mate in charge (Beissinger and Snyder 1987); and the third failed during incubation. Between successive attempts, kites moved distances as short as 100–300 m (the above female) or as far as 160 km (a male of 1978).

Some indication of the magnitude of multiple nesting attempts can be obtained by examining the data for 1978, when the kite population included a maximum of about 76 pairs (Fig. 1). In the following calculations we assume the accuracy of this census data and (1) a 1:1 sex ratio, (2) that all birds counted in late 1977 were potential breeders in 1978, and (3) that no birds died between the 1977 census and the end of the 1978 breeding season. During 1978 we documented 60 successful nesting attempts (not counting successful manipulated nests), but only 28.8% of the 52 attempts discovered at the nest-building stage were successful. By extrapolation, 60 successful nests were the surviving attempts from 208 nesting starts (of which we directly documented 136 nests). Thus the population averaged roughly 2.7 nesting attempts per pair in 1978. Note that although we refer to nesting attempts per pair, the actual makeup of pairs probably changed with many successive breeding attempts because of widespread mate desertion (Beissinger and Snyder 1987).

SURVIVAL OF FLEDGLINGS AND OLDER BIRDS

Survival of fledglings and older birds, at least under favorable water conditions, was extremely high. In 1979 we put radio transmitters on 13 nestlings, and all 13 were still alive more than a year later (Snyder et al. 1989). Furthermore, at another 21 nests studied closely through the post-fledging dependency period in 1979, 1982, and 1983, offspring mortality occurred in only one brood (Beissinger and Snyder 1987). These results suggest strongly that fledgling kites may face few predators and have little difficulty developing foraging skills when food is abundant. In close observations of the development of foraging abilities of fledglings, we found that they rapidly became as efficient as adults in locating and capturing snails, although they took somewhat longer to learn how to extract snails from shells efficiently. With a prey species normally as easy to procure as the apple snail, it is not surprising to find that survival of fledglings can be excellent under good food conditions. However, in 1981, a year of poor food, only two of four fledglings under close observation at two nests survived for 2 months after fledging (Beissinger 1986).

High survival of older birds was clear from resightings of banded individuals. Resightings yielded only minimum estimates of survival as only a fraction of birds alive in any year were checked for bands. Our most intensive efforts to locate banded birds were made in 1979, and the banded individuals known alive in this year can be used to calculate minimum annual survival rates for birds of various ages (Table 7). For many years these rates were impressively high (60–100%). Judging from the data of Sykes (1979, 1983a) and Beissinger (1986), most mortality probably occurred in drought years and was quite likely caused mainly by starvation and the dangers imposed by drought-related dispersal (Beissinger and Takekawa 1983). Nevertheless, at least seven of eight adult kites (87.5%) given radio transmitters in the drought year of 1981 survived into the study period of 1982. Under good conditions, the average annual survival rate of adults probably exceeds 90%.

AGE OF FIRST BREEDING

In 1979 we documented eight color-banded nesting yearlings. As we checked only 50.8% of the kites at nests for bands in 1979 and clearly did not find all nests in that year, there may actually have been, by extrapolation, more than 16 banded breeding yearlings. However, since 121 young were banded in 1978, and at least 74 of these survived in 1979, and since we believe that we likely found more than half the nests active in 1979, it also follows almost certainly that some birds that hatched in 1978 did not breed in 1979.

In 1980, a year in which we were able to make only very brief field studies, we also found one breeding yearling. Again in 1983, we found a breeding yearling, though we banded relatively few nestlings in 1982.

Of the 10 documented yearling breeders, six were females, judging from the plumage of their mates. We were unable to sex the other four. The youngest breeders were two females who started nests at only 277 and 279 days (9 months) of age, respectively. Most yearling breeders nested relatively late in the breeding season following their hatching year (nest-initiation dates ranged from 1 March to 27 May for nine of the 10 cases).

TABLE 7.   Banded Everglade Kites known alive in 1979 and their minimum survival rates.

Year of banding[a]	Total nestlings banded	Minimum number ostensibly surviving in 1979[b]	Allowing for band loss ambiguities[c]		Minimum annual survival (percent) since banding[d]
			Range of minimum numbers surviving in 1979	Range of minimum percent surviving in 1979	
1968	16	1	0–1	0–6	0–76
1969	6	3[e]	0–3	0–50	0–93
1970	9	3	2–4	22–44	83–90
1972	3	0	0–1	0–33	0–85
1973	13	2	1–6	8–46	65–88
1974	10	4	2–5	20–50	73–87
1975	2	2	2	100	100
1976	5	3	3–5	60–100	84–100
1977	1	0	0–1	0–100	0–100
1978	121	74	74–79	61–65	61–65

[a] Nestlings from 1968 through 1977 banded by Sykes (1979).
[b] Taking band combinations at face value and assuming no band loss.
[c] Calculations based on all possible ambiguities resulting from band loss (birds in earlier years were banded with fewer color bands than were birds in later years). Many ambiguities were removable through plumage (age) characteristics of banded individuals. Others were removable by reading aluminum band numbers.
[d] Range based on all possible ambiguities and calculated as a constant survival rate over the years.
[e] Actually four birds had apparent band combinations from 1969, but two different birds (one male and one female) had the same band combination, so clearly band loss occurred on at least one bird from another year (possibilities included 1973 and 1977).

Remarkably, nine of the 10 yearling breeders were successful in fledging young, although we emphasize that five cases involved nests found at the nestling stage, one was found at the post-fledging stage, and the other four (one of which failed) were found at the egg stage. The overall average success rate for nests initiated March through May of 1979, 1980, and 1983 was 48% ($n = 52$) for nests found at the egg stage. Thus, there was no sign of reproductive deficiencies in the yearlings.

Under good conditions, we strongly suspect that most kites become breeders by their second year. Unfortunately, we have not been able to test this question comprehensively. During both years when large numbers of banded 2-year-olds were presumably alive (1980 and 1981), practical constraints prevented us from examining many nesting pairs for bands. In 1980 our field efforts were limited to single days in February, April, and June, and several days in late July and early August. In 1981 extremely few pairs nested because of a drought. Nevertheless, in February 1980, we found seven of 17 breeding birds checked for bands to be known 2-year-olds, a proportion strongly suggesting widespread breeding at this age.

DISCUSSION

NESTING SUCCESS AND PRODUCTIVITY

Overall success of nests found at early stages (Table 2) was exceedingly low when compared with success figures for other raptors (Brown and Amadon 1968, Newton 1979). Furthermore, the figures in Table 2 are actually high estimates of natural nesting success because (1) the mid–late nestling period, rather than the end of the post-fledging dependency period, was taken as the endpoint of reproduction, and (2) lumping nests found during all portions of a stage (e.g., incubation) resulted in an upward bias because it does not account for unfound failures early in the stage. In addition, we found no evidence that any kite pairs ever worked on more than one nest simultaneously. Thus, high early failure rates were not an artifact of pairs reducing their nesting activities from plural to single sites. The conclusion is firm that overall natural nesting success of the Florida Everglade Kite has been consistently very poor.

In spite of dismal rates of nesting success, our study period was characterized by a large overall population increase (Fig. 1), punctuated by only two major declines during the drought years of 1971 and 1981 (when few nests were attempted). The reconciliation between poor natural nesting success and a substantial population increase is to be found primarily in high survival of free-flying individuals and several reproductive factors. First, the manipulated nests, which we considered to be uniform failures for calculations of natural nesting success, were actually fairly successful (47.8% successful from the egg stage), producing 99 young during the study period (Beissinger and Chandler, unpubl.). As this total accounts for 49.6% of the 127 young documented from 1966 through 1977, and 19.5% of the 507

young overall, it was an important component of the increase.

In addition, productivity was increased by renesting after failure, multiple brooding, and a system of mate desertion we have described in detail elsewhere (Beissinger 1986, 1987b; Beissinger and Snyder 1987). In years with good food supplies, virtually every successful nesting effort was characterized by desertion of one adult at about the time the young fledged. Such desertion did not reduce nesting success, but did result in one parent being free to start a new reproductive bout about a month sooner than would have been possible if both parents had attended the brood until independence. In most years, mate desertion would have increased the number of potential breeding attempts appreciably (Table 1).

In years of good food supplies, it is clear that most breeding kites make multiple nesting attempts and that productivity should not be considered solely in terms of nesting success. The 60 known successful nestings of 1978 (almost surely an underestimate) indicate that on average nearly every breeding kite produced young in that year (i.e., a net annual "nest success" rate approaching 100%), despite an overall success rate of only 30.6% in individual attempts. Multiple brooding and renesting are major components of overall productivity of the species.

FACTORS AFFECTING NESTING SUCCESS

Because of a chronic loss of an enormous amount of reproductive potential to nest collapse, one wonders why the Everglade Kite has not exhibited greater skills in choosing secure sites. That the success rate of manipulated nests was nearly 50% from the egg stage, as compared to an overall rate of 32% for unmanipulated nests, indicates clearly how much kites would stand to gain.

However, the common use of herbaceous nesting substrates in the lakes region may be due in part to the spatial segregation of good nest substrates from good foraging areas, and the strong tendency for the kites to build nests over relatively deep water. Woody vegetation generally grows only in shallow water while emergent herbaceous vegetation can tolerate greater depths (Pesnell and Brown 1977). During high water years, kites often nested in shrubs along lake margins, whereas in low water years nests were built mainly in cattails in central portions of the lakes. Beissinger (1986) suggested that kites nest over

water to avoid predation and gave evidence for high failure rates of nests which became dry underneath. Thus, during low water conditions kites tended to switch from stable nest substrates (where predation was likely to occur) to more unstable sites (where predation was less likely but where collapse was a major factor).

In part this choice may have been due to an interaction of food with nest-site availability. In low water years, the best foraging grounds on the lakes are sometimes two or more kilometers from the nearest substantial woody substrates. Everglade Kites feed on small food items relative to their body mass and carry these items singly, usually with flapping flight, back to their nests. Consequently, the energetic costs of commuting between nests and foraging grounds can be relatively expensive. Such costs very likely explain why we have sometimes seen Everglade Kites on Lake Okeechobee extracting snails from their shells while flying (contra Sykes 1987c), rather than carrying them to distant perches to extract them in the usual manner. Thus, the frequent nesting in cattails in the lakes region and the relatively poor nesting success in woody substrates, when they are used in this region, could be partly a result of foraging efficiency problems. In CA3A numerous willow "islands" are scattered throughout the principal hunting grounds, and kites are essentially never forced to use herbaceous nest substrates to be within efficient range of good hunting areas.

Nevertheless, since we occasionally saw kites using cattail nest sites within modest distances of woody substrates, we question whether the above explanations are totally satisfactory. Moreover, we sometimes saw kites repeatedly attempt to nest in the same poor crotches in willows, only to have their nests repeatedly fall, in spite of the presence of apparently better crotches in the immediate vicinity. Perhaps part of the problem lies in a need for kites to make direct aerial approaches to nest sites (probably dependent in part on their relatively long wings and extremely long talons). They do not walk or shuffle along perches to reach nests, and thus many crotches that to us appear superior to ones actually used by the birds may not really be usable. In contrast, the congeneric Slender-billed Kite (*R. hamatus*) characteristically walks or shuffles along limbs to its nests and is able to utilize subcanopy crotches in heavily forested areas for nesting. *Rostrhamus hamatus* is not

known to suffer chronic problems with nest collapse (Beissinger et al. 1988).

CLUTCH SIZE AND EGG HATCHABILITY

Overall clutch size in this study averaged 2.66 and was similar to values reported by Beissinger (1986) and Sykes (1987b) for modern clutches (2.71 and 2.75, respectively). This is a modest-sized clutch for a medium-sized raptor (Newton 1979). In addition, egg hatchability (80.9%) was very low by falconiform standards (Newton 1979). Both features indicate a relatively low reproductive potential for individual nesting attempts.

One of the most interesting results of the study was an absence of any discernible fluctuation in clutch size with widely varying water conditions (Table 5). Instead, the primary reproductive adjustments made by kites in poor food years appeared to be not breeding at all and avoidance of mate desertion in nesting attempts that were made (see Beissinger and Snyder 1987). Clutch size did not vary in the short-term. Possibly this constancy is in part a reflection of (1) difficulties that the kites have in predicting trends in food availability at the time of egg laying, and (2) the fact that clutch size is normally held low enough so that under good conditions one adult can raise a full brood, allowing routine mate desertion.

Nevertheless, clutch size was significantly higher on the lakes than in CA3A, and it is possible this was a food supply effect. Although we lack comprehensive data on comparative food availability in the two regions (no good methods for censusing *Pomacea paludosa* populations are known), the lakes have sufficient ranges of water depths that they do not normally become fully dry even in severe droughts. CA3A, on the other hand, became totally dry in several years during the study period. Since total dryouts cause obvious massive declines in snail numbers, snail populations may be more consistently vigorous in the lakes region than in CA3A.

CAUSES OF NESTING FAILURE

Our present analysis of reasons for nesting failure in the Everglade Kite is much more conservative than previous ones (e.g., Beissinger 1986, Sykes 1987b) in assigning specific causes. In most cases, unless one is in a nearby blind as failure occurs, causes cannot be determined with certainty. Even nest collapse, which we feel certain is a major problem, can be deceptive. Did the nest fall during or after failure? Or did it fall because it was disrupted by a predator, or because a heron picked it apart for nesting material after it was abandoned for other reasons? If we had not seen many active nests in the process of tipping over and failing, we might be less confident about the importance of this problem—it is one of the few causes of failure that often acts gradually enough to be detected by intermittent nest visits.

The classification scheme used to segregate potential causes of nesting failure (Table 6) is in the last analysis arbitrary and based on assumptions which may or may not be valid. Nevertheless, it has the considerable advantage of presenting ranges of probability for specific causes rather than simply fixed values of dubious accuracy. The breadth of these ranges are an indication of just how tentative the conclusions are.

Most commonly, failed nests have simply been empty and undisrupted when found and could have failed for a variety of reasons. We have had particular difficulty in separating failures possibly due to predation from those possibly due to desertion followed by scavenging (remembering here that desertion may not be so much a cause as a symptom of other ultimate problems). Thus, the relative importances of desertion and predation remain quite speculative.

By comparison, the evidence that many Everglade Kite nests have failed due to inadequate nest substrates is impressive. That we felt compelled to provide artificial supports for more than one-sixth of the nests found after 1972 is evidence enough of the severity of this problem. That we found another 68 nests that had apparently or possibly failed to this cause makes the case even more forceful. We know of no other raptors, with the possible exception of the Mississippi Kite (*Ictinia mississippiensis*), that have such chronic nest-collapse problems (Parker 1974, Glinski and Ohmart 1983), although some populations of Ospreys (*Pandion haliaeetus*) have suffered substantial losses from this cause (Dunstan 1968, Postupalsky and Stackpole 1974). Nest collapse has rarely been reported in buteos, accipiters, and other well-studied falconiform groups (Newton 1979).

To what extent could the high failure rate of kite nests early in the breeding cycle have been a result of the disturbance associated with nest checks? This question is difficult to evaluate rigorously, though we are skeptical that it has been a significant problem for two main reasons. First,

only five apparent rejection-desertions followed the relatively massive disturbance associated with placing 85 early-stage nests (many in the early egg-laying stage) in artificial baskets. Second, in analysis of 101 post-1978 nests found during nest building for which visitation data were unambiguous, failure by the egg stage was no more frequent in researcher-visited nests than in nests observed only from a considerable distance: 32% of 38 nests that were never visited directly failed by the egg stage, as compared with 38% of 63 nests that were visited one or more times during this period ($\chi^2 = 0.44$, df = 1, $P > 0.5$). These data strongly suggest: (1) no more than minor effects from human disturbance, and (2) that high rates of early nesting failure are a natural phenomenon.

SYNTHESIS OF EVERGLADE KITE DEMOGRAPHIC DATA

The important demographic characteristics of the Everglade Kite include (1) extremely low nesting success due in part to frequent nest collapse, frequent nest desertion and predation, and low hatchability of eggs, (2) extremely long breeding seasons, allowing multiple breeding attempts and multiple broods, (3) early attainment of sexual maturity, and (4) very high survival of juveniles and adults under favorable environmental conditions, but a high vulnerability to droughts due to an almost complete dependence on a single species of drought-sensitive snail for food.

That the habitat and food supply of the kite are highly unstable, both on a short- and long-term basis, is probably the main factor leading to reduced investment by the birds in individual nesting attempts and their utilization of a strategy of maximizing numbers of breeding attempts (Beissinger 1986, 1987a). Thus, the species maintains a low clutch size, making mate desertion possible under good conditions. Frequent nest desertion during early stages may represent an adaptive "cutting of losses" in an unpredictable environment (Low 1978, Beissinger 1986). Presumably it is better to move and try again than to persist in a given attempt if local conditions do not prove sufficiently encouraging.

The result of these breeding strategies and survival characteristics is that Everglade Kite numbers can expand very rapidly when good conditions prevail (Fig. 1). Despite low nesting success per individual attempt, the rate of population increase and the net annual "nesting suc-

cess" rate per bird have approached 100% in some recent years (via widespread mate desertion and multiple brooding). In years of somewhat poorer conditions, the species has exhibited considerable flexibility in breeding strategies, as some pairs have elected to forego mate desertion, and breeding seasons have shortened. Under severe drought conditions, most birds have not attempted breeding at all, and the few that have bred have not exhibited mate desertion, as breeding seasons have contracted still further and most birds have dispersed from traditional habitats in desperate attempts to find food elsewhere (Beissinger and Takekawa 1983).

In view of its enormous reproductive potential under good conditions, the kite is an unusual member of the endangered species fraternity, coming about as close as any diurnal raptor to being "r-selected" (sensu MacArthur and Wilson 1967, Boyce 1984). Its vulnerability to extinction comes mainly from its single-minded dietary habits and the sensitivity of its food supply to environmental fluctuations and overall habitat degradation.

OTHER STUDIES OF EVERGLADE KITE REPRODUCTION AND DEMOGRAPHY

Sykes (1979) presented data for 183 nesting attempts from 1968 to 1976, which included our data for 107 nesting attempts on Lake Okeechobee. His analysis led him to claim an overall nesting success rate of 48%. This estimate is almost five times as high as our 10% estimate of natural nesting success for the same period (from the nest-building stage), despite being based to a large extent on the same field data. The primary causes of the difference are: (1) Sykes included at face value 43 manipulated (basketted) nests on Lake Okeechobee, which were far more successful than unmanipulated nests and accounted for 20 of the 84 successful nests during the time period considered, (2) he included nests found at all stages of the breeding cycle, including a number found at the nestling stage, and (3) he omitted a substantial number of Lake Okeechobee nests from 1968–1976 that failed in the nest-building stage. Thus, his nest success figure is strongly biased toward the high side and is not a useful estimate of natural nest success.

In a later paper, Sykes (1987b) acknowledged the problem of including manipulated nests in his 1979 calculations and re-presented data for kite nesting success, this time including data from

29 nests of 1977 and 1978 as well, and now claiming an overall nest success rate of 50%. Nevertheless, even though he stated that he had now excluded all manipulated nests from calculations, examination of his nest totals for 1968 through 1976 indicated no changes from the totals presented in Sykes (1979). Thus, his 1987 paper does not represent any discernible change in methods of analysis from his 1979 paper. The great variety of reproductive success comparisons presented in Sykes (1979, 1987b) are of dubious validity because of these methodological problems in calculating nest success.

Nichols et al. (1980) presented a demographic model of the Everglade Kite based on the data of Sykes. Unfortunately, their calculations rested on a number of unsupportable assumptions: (1) that kites do not breed until 3 or 4 years old (our data indicate breeding at 1–2 years of age), (2) that they nest only once a year (our data indicate multiple attempts), (3) that their average production of young is 0.88 per nesting attempt (our data indicate 0.28 per attempt), and (4) that the average annual rate of population increase from 1969 to 1979 was 5.44% (we calculate an average annual increase of 15.7% for this period using their method—geometric mean), and that the 5.44% figure should be taken as a best estimate of the capacities of the species to increase (despite the fact that the 1969–1979 period included a massive drought and population decline in 1971, and a lesser drought and population decline in 1974). Their assumptions and calculations led these authors to characterize the kite as a species incapable of rapid population increases and highly resistant to declines under poor conditions (i.e., a highly "k" selected species, sensu MacArthur and Wilson 1967). Specifically, they calculated a maximum sustainable annual rate of increase of 24% (assuming no mortality of any age class) and a maximum rate of population decline of 7%.

In fact, the species has shown much greater declines in droughts, and, despite a low nest success rate, has shown much more rapid population increases under good conditions. Assuming the validity of the census data of Figure 1, the population exceeded the maximum rates of increase and decline calculated by Nichols et al. (1980) in 11 of the 14 years during our study period for which annual population change data are available.

Sykes (1987b:184) claimed that the breeding season of the Everglade Kite is timed to "take advantage of increasing seasonal water levels in Florida's marshes and avoid the period of intense local summer storms with heavy rain and strong winds. Most young had fledged when the rainy season commenced in May and water levels began to rise." However, our data indicate frequent nest initiations in 8 months of the year, including two of the hot summer months (June–July), and under a great variety of water and wind conditions (Table 4). With such a broad range of initiation dates it is difficult to tie breeding to specific seasonal rainfall characteristics, though the general absence of nest initiations in late summer and early fall has been quite consistent. We suspect that initiation of breeding is primarily dependent on food availability, which is in turn mainly a function of snail populations, water levels, and density of obscuring surface vegetation. The seasonal increase in surface vegetation in late summer and fall could be the primary factor causing a cessation of breeding, despite generally high snail populations through this period (Hanning 1978, pers. observ.), although this hypothesis has not yet been tested critically.

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