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THE ROLE OF PREDATION IN DETERMINING REPRODUCTIVE SUCCESS OF COLONIALLY NESTING WADING BIRDS IN THE FLORIDA EVERGLADES[1]

PETER C. FREDERICK AND MICHAEL W. COLLOPY
Department of Wildlife and Range Sciences, 118 Newins-Ziegler Hall, University of Florida, Gainesville, FL 32611-0304

Abstract. In a sample of 1,609 marked nests of five species of Ciconiiformes in 21 colonial nesting aggregations in the Everglades, evidence of abandonment without destruction of nest contents accounted for 31.3% of failures. In 66.9% of the failures, evidence at the nest suggested either predation resulting in nest failure or postabandonment scavenging of nest contents. In a sample of 106 nests isolated by a nonrepelling tracking medium, we found predation by snakes to account for 23% of nest failures; mammals accounted for an additional 20%. Failures due to these two categories accounted for 12% of the treated nests; abandonments may have been considerably underrepresented in this sample of nests. Mammalian predators rarely visited widely distributed baited tracking stations in the marsh, and we hypothesize that even 5–10 cm of water can substantially restrict travel by raccoons, foxes, and rats. Visitation by mammals to colonies occurred only when the water surrounding them receded, and was not related to the presence of alligators or distance from permanently dry land. We found little evidence of avian predation on wading bird nests, though birds readily scavenged abandoned nest contents. We discuss several attributes of the Everglades marshes which may limit access of predators to nesting colonies.

Key words: *Wading birds; nesting success; predation; colonial nesting; Ciconiiformes.*

INTRODUCTION

Nest predation generally is agreed to have played a central role in the evolution of many aspects of avian nesting behavior (Lack 1968, Hussell 1972, Burger 1982, Clark and Wilson 1981). One of the principal advantages of colonial nesting is the avoidance of nest predation via early warning, predator swamping, and group defense (Burger 1982, Wittenberger and Hunt 1985). Among Ciconiiformes, however, there is almost no group or individual nest-defense behavior, and even a small number of predators apparently are capable of destroying very large colonies (Baker 1940, Shields and Parnell 1986, Rodgers 1987). Instead, the avoidance of nest predation appears to be accomplished by selecting inaccessible nesting sites, often on islands surrounded by water.

Little is known, however, about the factors that limit access of mammalian, reptilian, and avian predators to wading bird colonies. Mammals, such as foxes (*Vulpes fulva* and *Urocyon cineroargenteus*) and raccoons (*Procyon lotor*), are usually nocturnal predators and are capable of rapid destruction of colonies, both through preying on nest contents and by causing the abandonment of nests not affected directly (Burger and Hahn 1977; Southern and Southern 1979; Rodgers 1980, 1987). Predation by mammals usually is reported from colonies at which the protective moat of water has dried during the course of nesting (Lopinot 1951, Rodgers 1987). The water depth or distance across water that actually limits access by semiaquatic mammalian predators have not been investigated.

Avian predators obviously are not limited by water barriers. Fish Crows (*Corvus ossifragus*), American Crows (*Corvus brachyrhynchos*), Black-crowned Night-Herons (*Nycticorax nycticorax*), and Great Horned Owls (*Bubo virginianus*) are the most frequently reported avian nest predators in wading bird colonies in the United States (Baker 1940, Dusi and Dusi 1968, Jenni 1969, Nisbet 1975, Burger and Hahn 1977, Burger 1982, Pratt and Winckler 1985, Shields and Parnell 1986, Bancroft and Jewell 1987). All are commonly found, even on remote offshore island colonies. Recorded rates of nest predation by birds vary considerably among colony sites (see Shields and Parnell 1986 and Frederick 1987), and it is not known why some colonies are more affected by avian predators than others.

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Several species of snakes are predators of eggs and have been suggested to cause significant nest mortality in wading bird colonies (Dusi and Dusi 1968, Jenni 1969, Taylor and Michael 1971). Nest failures due to snake predation, however, are difficult to detect and distinguish from post-abandonment egg scavenging. Thus far, no quantitative study of the importance of snake predation in wading bird colonies has been completed. In this paper we report on the importance of nest predation by birds, mammals, and snakes in mixed-species wading bird colonies in the Everglades of southern Florida, and comment on factors affecting the distribution and abundance of nest predators in this extensive freshwater marsh ecosystem.

STUDY AREA AND METHODS

We systematically searched for wading bird colonies in Everglades National Park (ENP) and Water Conservation Area 3 (WCA 3, see Fig. 1) from 1 January through 31 July in 1986 and in 1987, using both aerial and airboat survey methods (see Frederick and Collopy 1988 for survey details). Thirty-seven and 44 colonies, respectively, were active in 1986 and 1987, for a total of 81 nesting events at 56 locations (nesting events occurred at some locations in both years). We visited 40 of these nesting events on the ground at least once, and selected 11 in 1986 and 10 in 1987 for detailed study of nesting success; a total of 18 colony locations were monitored (three sites were studied in both years). We selected these colonies for study because they were large, had mixed-species composition, were geographically representative of a large percentage of the study area, and did not have endangered Snail Kites (*Rostrhamus sociabilis*) nesting in them.

We marked individual nests with numbered strips of surveyor's tape and visited them once every 4 days until the nest succeeded (produced at least one young capable of walking escape) or failed. Eggs were marked with a letter on the large end, using a laundry marking pen, to ensure that eggs lost and replaced between visits were detected. Nests too tall for us to reach by climbing were inspected using a mirror pole; eggs in these nests also were marked using a wide-tipped marker attached to the mirror pole.

Predation was defined as the destruction of nest contents while the nest was still active. This was distinguished from scavenging, in which the contents of nests were destroyed or consumed only after the nest had been abandoned for other reasons. The disappearance of single eggs from a still-warm clutch (and absence of whole eggs on the ground beneath, suggesting the egg fell or was kicked from the nest) was considered evidence that the missing egg was eaten by a predator. Loss of entire clutches was considered ambiguous, since this could have resulted either from predation followed by abandonment, or abandonment for other reasons followed by scavenging of nest contents. Even when eggs obviously damaged by birds or mammals were found on the ground or in the nest, we could not necessarily attribute the primary cause of damage to predation, since it also could have resulted from postabandonment scavenging. Abandonment not induced by predation was assigned only when a complete set of cold eggs was found during the incubation period, or when a complete brood was found dead or moribund in the nest.

In 1987, we implemented two methods to bet-

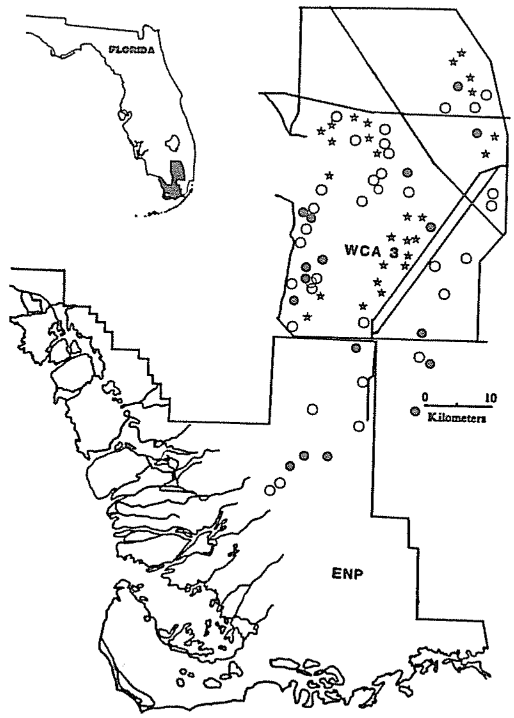

FIGURE 1. Map of southern Florida, showing boundaries of Water Conservation Area 3 (WCA 3), and Everglades National Park (ENP). Locations of colonies found during the 2-year study are shown by circles; filled circles represent those studied through repeated nest-check visits. Locations of predator tracking stations are shown by stars.

ter elucidate the importance of predation at nests. To obtain evidence of snakes, mammals, and other predators that must climb trees in order to gain access to nests, we sprayed Tanglefoot (a gummy, nontoxic foam used to trap crawling insects; The Tanglefoot Company, Grand Rapids, Michigan) on the trunks of trees and branches supporting the nests we marked for study. In the sprayed form, Tanglefoot leaves a sticky, foamed surface on bark, and even a slight disturbance results in recognizable marks. Light to moderate rainfall did not mar the foamy surface. Tanglefoot contains largely inert ingredients; we observed two campground raccoons repeatedly cross Tanglefoot barriers to obtain food. On initial and subsequent exposures, two captive rat snakes (*Elaphe obsoleta obsoleta* and *E. o. quadrivittata*) repeatedly crossed Tanglefoot patches with no sign of avoidance behavior. We therefore doubt that Tanglefoot was a deterrent to potential climbing predators. We only treated nest trees in which the nest could be reached by a few isolated branches or trunks, and resprayed any areas that had been disturbed. The entire circumference of trunks and branches was covered with Tanglefoot for a minimum of 45 linear cm. We treated 106 nest trees in six colonies, and followed the fates of these nests from 1 April to 30 May 1987.

We also attempted to estimate the relative abundance of potential mammalian predators in the freshwater Everglades by attracting mammals to baited tracking stations. In May 1986, we placed opened cans of sardines and broken chicken eggs in cleared areas of high ground in a single large willow (*Salix caroliniana*) stand in the northeastern part of WCA 3 in which Great Egrets (*Casmerodius albus*) had recently been nesting.

From 15 March to 15 May 1987, we repeatedly checked plywood tracking stations at 27 locations in WCA 3 representing both deep and shallow water depths (Fig. 1). These stations were 70-cm diameter discs of plywood, painted and varnished on one surface, and mounted horizontally on a PVC pole 4 to 6 cm above the water surface. Each station was baited with an opened can of sardines, which was fastened to the middle of the plywood disc. The bait was covered by a 15-cm section of aluminum gutter pipe, left open at both ends. Stations were placed on the edge of willow tree islands that were not being used by nesting wading birds, and that varied in size from 0.2 ha to over 7 ha. These tree islands were typical of wading bird nesting habitat in the Everglades (Frederick and Collopy 1988). Stations were checked once every 4 days, and brushed with blue chalk dust to make any tracks visible (Humphrey and Zin 1982). If the station had been visited by a potential nest predator, we subsequently moved the station to a different willow head located a minimum of 1 km away.

Water depths were measured at each bait station using a standardized 1,000-g pole, and read on its side after allowing it to fall by its own weight into the marsh substrate. At each tracking station, 20 measurements were taken in each of the two nearest prairies to the east and west of the station that were dominated by rushes of the genus *Eleocharis*. Means of these measurements were used as indicators of water depths in the vicinity of the stations.

RESULTS

In the entire sample of nests studied in both years, direct evidence of abandonment was found at 33.3% of the failed nests (Table 1). Direct evidence of predation was found infrequently (2.5% of failed nests, between 2.5% and 5.7% of eggs, Table 2); in both years a very large proportion of nests was found empty (62.8% combining both years) with little clue as to the cause of failure. Thus, while evidence at the nest suggested nest predation was minor, the existence of the large unknown category made this conclusion highly speculative.

In the sample of 106 nest trees marked with Tanglefoot, 35 showed some disturbance; of these, 16 were marked either by the brushing of nearby vegetation or were tracked by herons approaching their nests from below (a behavior frequently reported by Jenni 1969). Among the remaining 19 cases, seven trackings were attributable to snakes, one to an otter (*Lutra canadensis*; confirmed by scat at the base of the tree), and 11 were unidentifiable.

Thirty (28%) of the 106 nests we marked with Tanglefoot failed. Of the 19 nests where Tanglefoot was disturbed, 13 (68%) failed. Predation by snakes, mammals, or other climbing predators therefore could have accounted for as many as 13 of the 30 failures (43%) and been the cause of failure at 13 of the sample of 106 nests marked (12%). Predation specifically by snakes could have accounted for 23% of the failures, and might have caused the failure of as many as 7% of the treated nests. At the 17 failed nests with undisturbed

TABLE 1. Sources of nest failı

Year	Sı
1986	White Ibis
	Great Egret
	Tricolored]
	Little Blue]
	Snowy Egre
Annual total	
1987	White Ibis
	Great Egret
	Tricolored]
	Little Blue]
	Unidentifie
Annual total	
Grand total	

[1] Handling by observers, wind damage, r
[2] Unidentified nests of three *Egretta* spec

Tanglefoot, nest contents were preyed upon or scavenged by the paucity of avian nest pre suspect that the majority of tl abandonment scavenging (56

In 1986, we never saw sna spite over 400 man-hours searching foliage for nests. In man-hours in colonies, and snakes in colonies on four o onies) and cottonmouth moc *piscivorus*) on four occasions of the rat snakes were estima cm in length, and probably la low eggs of Great Egrets. Un none of the cottonmouths w the latter are probably too h arboreal predators.

TABLE 2. Partial loss of clutcl iformes in freshwater marshes o

Species
Great Egret
White Ibis
Tricolored Heron
Little Blue Heron
Black-crowned Night-Heron
Great Blue Heron
Snowy Egret

[1] From date of first egg to 6 days later.
[2] From end of egg-laying period (1) to ha
[3] No data collected.

TABLE 1. Sources of nest failure identified during repeated nest checks.

Year	Species	Total failed nests	Primary cause of failure: Abandonment	Predation	Other[1]	Unknown (% of failures)
1986	White Ibis	168	67	0	1	100 (59.5)
	Great Egret	187	72	0	0	115 (61.5)
	Tricolored Heron	78	60	0	0	18 (23.1)
	Little Blue Heron	7	1	0	0	6 (85.7)
	Snowy Egret	2	0	0	0	2 (0.0)
Annual total		442	200	0	1	241 (54.5)
1987	White Ibis	90	45	8	3	34 (35.4)
	Great Egret	147	6	9	0	132 (89.8)
	Tricolored Heron	66	18	2	2	44 (66.6)
	Little Blue Heron	21	0	0	1	20 (95.2)
	Unidentified small herons[2]	60	1	2	5	52 (86.7)
Annual total		384	70	21	11	282 (73.4)
Grand total		826	270	21	12	523 (63.3)

[1] Handling by observers, wind damage, nest usurpation by other species.
[2] Unidentified nests of three *Egretta* species.

Tanglefoot, nest contents were likely to have been preyed upon or scavenged by birds; considering the paucity of avian nest predators (below), we suspect that the majority of these cases was post-abandonment scavenging (56% of failures).

In 1986, we never saw snakes in colonies, despite over 400 man-hours spent in colonies searching foliage for nests. In 1987, we spent 350 man-hours in colonies, and found yellow rat snakes in colonies on four occasions (three colonies) and cottonmouth moccasins (*Agkistrodon piscivorus*) on four occasions (two colonies). All of the rat snakes were estimated to be over 100 cm in length, and probably large enough to swallow eggs of Great Egrets. Unlike the rat snakes, none of the cottonmouths were found in trees; the latter are probably too heavy-bodied to be arboreal predators.

Exclusive of the Tanglefoot trackings, we found evidence of mammalian predation on five of our colony visits (four of the 18 colony locations visited repeatedly), and evidence of mammalian activity within 100 m of colonies on two other occasions (one additional colony site). Except for the single case involving an otter, all the evidence of mammalian activity suggested raccoons (scat, condition of eggs eaten, and tracks; see Rearden 1951). During the periods of raccoon activity, the marsh surface surrounding all of the five colonies was nearly dry (occasional surface pools of less than 5 cm). Presence of mammals in or near colonies was not related to the distance from the nearest permanently dry ground (Table 3) and mean distances to high ground were not significantly different between the entire group of colonies found and the sample of those we visited.

TABLE 2. Partial loss of clutches during egg laying and early incubation at nests of seven species of Ciconiiformes in freshwater marshes of southern Florida.

Species	Egg laying[1] 1986 Eggs present	Egg laying 1986 % loss	Egg laying 1987 Eggs present	Egg laying 1987 % loss	Incubation[2] 1986 Eggs present	Incubation 1986 % loss	Incubation 1987 Eggs present	Incubation 1987 % loss
Great Egret	37	0	20	10.00	224	11.16	241	1.25
White Ibis	207	0	342	2.34	298	11.07	383	4.17
Tricolored Heron	282	0.71	755	0.79	652	3.83	965	1.96
Little Blue Heron	187	0.53	384	0.26	604	3.64	579	2.25
Black-crowned Night-Heron	44	0	4	0	82	3.66	21	9.52
Great Blue Heron	—[3]	—	—	—	—	—	75	4.00
Snowy Egret	20	0	—	—	82	3.66	—	—

[1] From date of first egg to 6 days later.
[2] From end of egg-laying period (1) to hatching of first egg.
[3] No data collected.

TABLE 3. Distances from all colony locations to nearest permanently dry land in WCA 3 and ENP.

		Distance (km)	
	n	$\bar{x}$[1]	SD
A. All colonies located	56	5.07	3.833
B. Colonies studied	18	4.99	3.834
C. Colonies studied where mammalian activity was noted	5	7.10	4.469
D. Colonies studied where mammalian activity was not noted	13	4.17	3.208

[1] No significant differences found between mean distances of any colony groupings; A vs. B, $t = 0.078$, $P > 0.90$; C vs. D Mann-Whitney $U = 21$, $P > 0.10$.

Presence of alligators (*Alligator mississippiensis*) could have been a deterrent to mammalian entry into wading bird colonies (Jenni 1969). We found evidence of recent alligator activity (i.e., territorial vocalizations, recent tracks, scat, and direct observation) within the colony perimeter at 15 of the 18 colony locations we visited repeatedly (80%). Five of the six total cases of mammalian activity also were in or near colonies where we had noted concurrent alligator activity.

The results of the tracking station survey suggested that mammalian predators were sparsely distributed in the Everglades marshes, and that their use of the marsh may be limited to very shallow water areas. No tracks were found at the hammock site baited in 1986. In 1987, the tracking stations were exposed for a total of 341 station-days, and checked for tracks on 68 occasions. They were located in both deep water (13 locations, $\bar{x}$ depth = 65.6 cm) and shallow water (14 locations, $\bar{x}$ depth = 15.8 cm) areas. Stations were visited on five occasions by potential nest predators—once by an otter, once by a raccoon, and on three occasions by unidentified medium-sized mammals (mink *Mustela vison* or larger). Other visits were made by unidentified small rodents ($n = 9$), an alligator, and unidentified anurans ($n = 28$). The small sample of all visitations by potential nest predators ($n = 5$) did not allow analysis of visitation in relation to water depths.

We found avian egg predators to be rare in the freshwater marshes of our study area. American Crows were seen (or heard) on only three occasions at one of the 40 colonies we visited at least once, despite over 750 total man-hours spent in colonies. Boat-tailed Grackles (*Quiscalus major*) and Red-winged Blackbirds (*Agelaius phoeniceus*) were commonly seen at wading bird colonies and often nested there. We observed a Purple Gallinule (*Porphyrula martinica*) eating an egg in an active nest after our approach had flushed the incubating Tricolored Heron (*Egretta tricolor*). Jenni (1969) also observed Purple Gallinules eating eggs, but only when parent birds were absent from nests. We never found evidence of Great Horned Owl predation of young or adults (Nisbet 1975, Pratt and Winkler 1985), and observed Red-shouldered Hawks (*Buteo lineatus*) in the vicinity of three colonies (three total occasions). Black-crowned Night-Herons were found nesting in three of the 40 colonies visited at least once, and we found evidence of this species eating chicks of White Ibises (*Eudocimus albus*) in two of those colonies. In both cases, however, the ibises were abandoning their nests at the time that we discovered the heron depredations, and it was not clear if the night-herons were acting as predators or scavengers. Both Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) were seen at wading bird colonies following 10 of 21 synchronous nest abandonment events (see Frederick and Collopy, in press). In all cases vultures appeared to be scavenging contents of nests that had already failed.

DISCUSSION

The estimates of nest predation derived from the Tanglefoot disturbances probably overestimate nest failure due to predation in both an absolute and relative sense. First, we were unable to identify tracks in the majority of the cases of disturbed Tanglefoot (58%); these cases might not have been related to nest failure, even though they were treated as such when tallied. These trackings could have been made by scavengers that were attracted to nests following failure of the nest for other reasons. Second, all Tanglefoot treatments were conducted between 1 April and 30 May, when synchronized large-scale abandonments of colonies did not occur (Frederick and Collopy 1988). Finally, the majority of the nests with the Tanglefoot treatments were of species that were least prone to abandonment (three species of genus *Egretta*; see Frederick and Collopy, in press). In short, the evidence of snake and mammalian predation is somewhat overestimated, and the importance of abandonment was considerably underrepresented by the sample of nests we treated with Tanglefoot. Both types of errors would tend to overestimate the

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importance of predation in determining nesting success. Even given this overestimation, the relative importance of nest failure due to abandonment (31.3% conservatively estimated in the total sample of nests, 56% in the Tanglefoot nests), in comparison to predation (liberally, 43% in Tanglefoot nests) was striking. The mechanisms by which nest abandonment (not induced by damage to nest contents) occurs are poorly understood, but are probably related to fluctuations in food availability (Frederick and Collopy, in press).

Rat snakes are the most likely reptilian nest predators in the Everglades. They are well-known egg and chick predators (Conant 1975, Bennetts and Caton 1988) and have often been reported in wading bird colonies in the southeastern U.S. (Dusi and Dusi 1968, Jenni 1969, Taylor and Michael 1971). They are probably the only species of snake in the Everglades that is sufficiently arboreal, large enough to swallow most ciconiiform eggs, and aquatic enough to travel long distances across water to colonies. Given the low number of snake sightings relative to search time, we suspect that the majority of snake predation is accomplished by one or a very few individuals in each colony.

The ability of mammalian predators, particularly raccoons, to gain access to wading bird colonies appears to be directly limited by the presence of water. Raccoons and gray foxes frequently were seen along roads and dikes surrounding the study area but evidence of raccoons in and around colonies was only found when colonies were surrounded by dry marsh surface. Raccoon activity did not appear related to either distance from the colony to permanently dry land or the presence of alligators. It was surprising that raccoons were not using the comparatively shallow marshes (5–10 cm depth) near many of our tracking stations, suggesting that relatively shallow water can have an important dampening effect on nest predation.

Our evidence also suggests that birds are rarely predatory on wading bird nests, though they probably often scavenge nest contents. Vultures, grackles, Red-winged Blackbirds, and gallinules all were common in colonies, but probably are not capable of displacing adult herons from their nests; opportunities for these birds to prey upon eggs or nestlings are likely to be limited to periods of absence by both members of the pair (Jenni 1969), a rare situation in most ciconiiforms prior to the late nestling period (Jenni 1969; Weise 1975; Rudegeair 1975; Rodgers 1978, 1980; Frederick 1985, 1987). The effects of these scavengers on nest success may only become important during major colony disturbances, such as by human observers (Milstein et al. 1970, Shields and Parnell 1986).

Black-crowned Night-Herons were the only avian predators of nestlings we identified. Night-herons generally are limited to taking chicks less than 1 week old (Hancock and Kushlan 1984, Frederick 1985, Bjork 1986) and, in this study, probably scavenged White Ibis chicks from already abandoned nests. Their impact as predators is therefore difficult to assess. We suspect that Red-shouldered Hawks are not important nest predators because they were infrequently seen in colonies, and because birds generally make up less than 20% of their diet (Sherrod 1978).

Other potential predators such as crows and Great Horned Owls were exceedingly rare in the study area. American Crows frequently were seen on roads and dikes surrounding both WCA 3 and ENP, and were important nest predators in wading bird colonies located in the coastal mangrove zone of ENP (Bancroft and Jewell, unpubl.) and in Florida Bay (G. Powell, unpubl.). Their absence in freshwater colonies less than 15 km away therefore was striking. The distribution of crows may be dependent on the stability of wading bird colonies as food sources from season to season. Colonies in Florida Bay and the coastal section of ENP are active more consistently than most freshwater marsh colonies (Kushlan 1977, Kushlan and White 1977, Ogden 1978), making them much more predictable food sources. The only freshwater colony where we observed American Crows was less than 2 km from a major road (U.S. 41) where garbage and roadkills were available consistently.

Nest predation by mammals has evidently played an important role in the evolution of colony-site selection criteria. All colonies we found were surrounded by water of at least 30 cm depth at the time of formation. Despite the many types of tree islands available in the Everglades (Olmsted and Loope 1984), 85% of the colonies that we found were in nearly monospecific stands of willow. This type of tree island usually is found in areas with deep water, and in this ecosystem probably occurs in the deepest water available in any area (McPherson 1973). The importance of surrounding water in limiting access of mammalian predators seems well supported by this study; whether nest predation by birds can be affected by colony-site choice (degree of geographic isolation, consistency of site usage) seems an important direction for future research.

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LITERATURE CITED

BAKER, R. H. 1940. Crow predation on heron nesting colonies. Wilson Bull. 52:124–125.

BENNETTS, R. E., AND E. L. CATON. 1988. An observed incident of Rat Snake predation of Snail Kite (*Rostrhamus sociabilis*) chicks in Florida. Fla. Field Nat. 16:14–16.

BJORK, R. 1986. Reproductive ecology of selected Ciconiiformes nesting at Battery Island, North Carolina. M.Sc.thesis. Univ. of North Carolina, Wilmington.

BURGER, J. 1982. The role of reproductive success in colony site selection and abandonment in Black Skimmers (*Rhynchops niger*). Auk 99:109–115.

BURGER, J., AND C. HAHN. 1977. Crow predation on Black-crowned Night Heron eggs. Wilson Bull. 89: 350–351.

CLARK, A. B., AND D. S. WILSON. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. Q. Rev. Biol. 56:253–277.

CONANT, R. 1975. A field guide to the reptiles and amphibians of eastern and central North America. Peterson Field Guide Series. 2nd ed. Houghton Mifflin, Boston.

DUSI, J. C., AND R. T. DUSI. 1968. Ecological factors contributing to nesting failure in a heron colony. Wilson Bull. 80:458–466.

FREDERICK, P. C. 1985. Mating strategies in White Ibis (*Eudocimus albus*). Ph.D.diss. Univ. North Carolina, Chapel Hill.

FREDERICK, P. C. 1987. Chronic tidally-induced nest failure in a colony of White Ibises. Condor 89: 413–419.

FREDERICK, P. C., AND M. W. COLLOPY. 1988. Reproductive ecology of wading birds in relation to water conditions in the Florida Everglades. Florida Coop. Fish and Wildl. Res. Unit, School For. Res. and Conserv., Univ. of Florida Tech. Rep. No. 30.

FREDERICK, P. C., AND M. W. COLLOPY. In press. Nesting success of five species of wading birds in relation to water conditions in the Florida Everglades. Auk.

HANCOCK, J., AND J. A. KUSHLAN. 1984. The herons handbook. Harper and Row, New York.

HUMPHREY, S. R., AND T. L. ZINN. 1982. Seasonal habitat use by river otters and the Everglades mink in Florida. J. Wildl. Manage. 46:375–381.

HUSSELL, D.J.T. 1972. Factors affecting clutch size in arctic passerines. Ecol. Monogr. 42:317–364.

JENNI, D. A. 1969. A study of the ecology of four species of herons during the breeding season at Lake Alice, Alachua County, Florida. Ecol. Monogr. 39:245–270.

KUSHLAN, J. A. 1977. Population energetics of the American White Ibis. Auk 94:114–122.

KUSHLAN, J. A., AND D. A. WHITE. 1977. Nesting wading bird populations in southern Florida. Fla. Sci. 40:65–72.

LACK, D. 1968. Ecological adaptations for feeding in birds. Methuen and Co., London.

LOPINOT, A. C. 1951. Raccoon predation on the Great Blue Heron, *Ardea herodias*. Auk 68:235.

MCPHERSON, B. F. 1973. Vegetation in relation to water depth in Conservation Area 3, Florida. Open File Report, U.S. Geological Survey, Tallahassee.

MILSTEIN, P. LES., I. PRESTT, AND A. A. BELL. 1970. The breeding cycle of the Grey Heron. Ardea 58: 171–257.

NISBET, I.C.T. 1975. Selective effects of predation in a tern colony. Condor 77:221–226.

OGDEN, J. C. 1978. Recent population trends of colonial wading birds on the Atlantic and Gulf coastal plains, p. 135–153. *In* A. Sprunt, IV, J. C. Ogden, and S. Winckler [eds.], Wading birds. Natl. Audubon Soc. Res. Rep. 7.

OLMSTED, I., AND L. L. LOOPE. 1984. Plant communities of Everglades National Park, p. 167–184. *In* P. J. Gleason [ed.], Environments of South Florida, past and present II. Miami Geological Society, FL.

PRATT, H. W., AND D. W. WINKLER. 1985. Clutch size, timing of laying and reproductive success in a colony of Great Blue Herons and Great Egrets. Auk 102:49–63.

REARDEN, J. E. 1951. Identification of waterfowl nest predators. J. Wildl. Manage. 15:386–395.

RODGERS, J. A., JR. 1978. Breeding behavior of the Louisiana Heron. Wilson Bull. 90:45–59.

RODGERS, J. A., JR. 1980. Little Blue Heron breeding behavior. Auk 97:371–384.

RODGERS, J. A., JR. 1987. On the antipredator advantages of coloniality: a word of caution. Wilson Bull. 99:269–270.

RUDEGEAIR, T. J. 1975. The reproductive behavior and ecology of the White Ibis (*Eudocimus albus*). Ph.D.diss. Univ. of Florida, Gainesville.

SHERROD, S. K. 1978. Diets of North American Falconiformes. Raptor Res. 12:49–121.

SHIELDS, M. A., AND J. PARNELL. 1986. Fish Crow predation on eggs of the White Ibis at Battery Island, North Carolina. Auk 103:531–539.

SOUTHERN, L. K., AND W. E. SOUTHERN. 1979. Absence of nocturnal predator defense mechanisms in breeding gulls. Colonial Waterbirds 2:91–101.

TAYLOR, R. J., AND E. D. MICHAEL. 1971. Predation

on an inland heronr

Bull. 83:172–177.

WEISE, J. H. 1975. The

Great Egret *Casmero*

M.Sc.thesis. Florida S

on an inland heronry in eastern Texas. Wilson Bull. 83:172–177.

WEISE, J. H. 1975. The reproductive biology of the Great Egret *Casmerodius albus egretta* (Gmelin). M.Sc.thesis. Florida State Univ., Tallahassee.

WITTENBERGER, J. F., AND G. L. HUNT, JR. 1985. The adaptive significance of coloniality in birds, p. 1–78. *In* D. S. Farner, J. R. King, and K. C. Parkes [eds.], Avian biology. Vol. VIII. Academic Press, New York.