Habitat Variables Affecting Nesting Success of the American Alligator in Florida

Michael L. Jennings, *Florida Cooperative Fish and Wildlife Research Unit, Department of Wildlife and Range Sciences, University of Florida, Gainesville, FL 32611*

H. Franklin Percival, *Florida Cooperative Fish and Wildlife Research Unit, Department of Wildlife and Range Sciences, University of Florida, Gainesville, FL 32611*

C. L. Abercrombie, *Department of Sociology, Wofford College, Spartanburg, SC 29301*

Abstract: Five aerially estimated habitat variables and nest spacing patterns were used to develop predictive models for evaluating the status of American alligator (*Alligator mississippiensis*) nests on 2 lakes in central Florida. Models developed from data on 146 and 54 nests on Orange Lake and Lake Woodruff, respectively, indicated that none of the habitat variables were useful in predicting nest success. Nests occurred in clumped distributions in some years, but were not clumped in the same areas from year to year. Until more reliable methods for evaluating nest status are available, management programs that utilize alligator eggs should target the most accessible nests.

Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 41:334–342

Crocodilian ranching (the harvest and captive rearing of wild eggs and hatchlings) has become a viable enterprise (Natl. Res. Council 1983, Rose 1982). The concept of value-added conservation (using the monetary value of wildlife to encourage and finance conservation) has become an integral facet of some research and management philosophies (Hines and Percival 1987). American alligator ranching in Florida is being investigated as an addition to the established programs of adult harvest.

Hines et al. (1986) indicated that egg removal from many Florida alligator nests was the most efficient and effective harvest strategy for early age-classes, both from ecological and economic perspectives. In experimental harvests, entire clutches are taken from the most accessible nests. This procedure ignores the possibility of differential nest success and assumes random distribution of nest failure.

Nest failure can usually be attributed to flooding or depredation. The impact of each on total nest success varies among wetland systems (Joanen 1969, Metzen 1977, Deitz and Hines 1980, Wilkinson 1983, Jacobsen and Kushlan 1986). Throughout much of the alligators range, however, raccoons (*Procyon lotor*) are considered the predominant cause of nest failure (Joanen 1969, Fleming et al. 1976, Goodwin and Marion 1978, Dietz and Hines 1980). If the probability of nest depredation is variable, then harvest strategies should target those nests with the lowest probabilities of survival, reducing the impacts on alligator populations.

Aerial surveys have been used extensively for monitoring crocodilian nesting (Joanen 1969, Goodwin and Marion 1978, Webb et al. 1983). However, the majority of information has been used *post facto* to describe crocodilian nesting effort and success. To evaluate the potential for predicting future nest predation, we examined the possibility of developing models based on aerial surveys, that could be used to identify nests with high risks of predation. Specifically, our objectives were to: (1) determine if 5 habitat variables estimated at alligator nest sites during helicopter surveys would be useful in predicting whether nests would be depredated, and (2) determine, by aerial survey, the distribution of depredated nests at 2 lakes in central Florida from 1980 to 1985.

The Florida Game and Fresh Water Fish Commission provided equipment and computer facilities. R. F. Labisky, A. R. Woodward and T. C. Hines provided technical assistance and reviewed earlier drafts of the manuscript. T. C. Edwards contributed ideas for statistical analyses and computer programming. A. T. Bush and J. D. Defazio provided logistical support, and D. E. Carlberg provided helicopter service. This publication is a contribution to the Florida Agricultural Experiment Station, Journal Series 8382.

Methods

Study Areas

Orange Lake is a 5,175-ha, shallow lacustrine, aquatic bed lake (Cowardin et al. 1979), with a 1,820-ha littoral zone, located 32 km south-southeast of Gainesville, Alachua County, Florida. Characteristic marsh vegetation included: spatterdock (*Nuphar luteum*), hydrilla (*Hydrilla verticillata*), water hyacinth (*Eichhornia crassipes*), smartweed (*Polygonum* spp.), sawgrass (*Cladium jamaicense*), and pickerelweed (*Pontederia cordata*). Common shoreline trees were red maple (*Acer rubrum*), bald cypress (*Taxodium distichum*), Carolina willow (*Salix caroliniana*), and blackgum (*Nyssa sylvatica*). Alligator transect data for Orange Lake indicated minimum densities from 16.1 to 21.2 alligators per kilometer of shoreline (Wood et al. 1985). The number of nests established on Orange Lake from 1979 to 1983 averaged 83 annually, with the highest densities traditionally occurring in the southeast, southwest, and northern marshes.

Lake Woodruff, actually a complex of wetlands, is characterized as a small, 2,150 ha, lacustrine, aquatic bed lake (Cowardin et al. 1979) with a narrow littoral zone; it is located 20 km north of De Land, Volusia County, Florida. Characteristic vegetation of open water in the complex included coontail (*Ceratophyllum demersum*), the dominant submergent species; banana waterlily (*Nymphoides aquatica*); and spatterdock. Sand cordgrass (*Spartina bakeri*) was dominant in extensive marsh areas. Lake Woodruff maintains a moderate alligator population represented by an average of 10.9 alligators per kilometer of shoreline (Wood et al. 1985). Nesting averaged 43 annually from 1981 to 1984.

Surveys

Three aerial surveys were conducted at approximately 4-week intervals during mid-July through early September 1984 and 1985, from a helicopter. Nests located on the initial survey were mapped on aerial photographs (1:24,000), classified as either active or depredated, and photographed. Second and third surveys were conducted to determine nest status during late incubation and posthatching periods, respectively.

An active nest was distinguishable as an intact dome approximately 1.5 m in diameter and 0.5 to 1.0 m in height (Joanen 1969, Goodwin and Marion 1978). Active nests that hatched and were located during posthatching surveys were reclassified as successful. Successful nests typically have a semicircular excavation from the top center down to the bottom of the egg cavity, sloping broadly out and down to the side (Deitz and Hines 1980). Depredated nests were typically flattened, with nest material scattered, and alligator eggs or shell fragments littering the immediate area. Occasionally, only small holes on the nest top indicated depredation.

Habitat Variables

Five habitat variables were estimated from the aerial surveys: (1) percentage of nest shade, (2) height of the nesting substrate above water level, (3) vegetation density surrounding nest sites, (4) distance (m) of a nest to the nearest permanent shoreline, and (5) distance (m) of a nest to the nearest open water. Shade, estimated from directly above a nest, represented the proportion of nest shaded during the period of highest solar radiation. Percent shade was recorded in increments of 10, ranging from 0 to 100. Height was subjectively determined during the first flight. Nests constructed on an elevated substrate (dike or levee) were placed in height category 1; those on substrates indicative of "dry" marsh habitats (accessible by walking) were given a value of 2; and nests on unconsolidated substrate or floating mats of vegetation were assigned a value of 3. Vegetative density was evaluated for each nest from aerial photographs, and assigned 1 of 3 hierarchical values established *a priori* from a reference collection: 1 = sparse vegetative cover, 2 = intermediate cover, and 3 = dense cover. The reference collection for vegetative density was determined by the proportion of a 3-m index board (Hayes et al. 1981) that was obstructed by vegetative cover when photographed at a distance of 10 m from the nest. Any 0.25-m segment of the index board that was obscured by more than 50% was recorded as totally covered. Distances of a nest to the nearest permanent shoreline and to the water were estimated aerially and adjusted using aerial photographs.

Spacing Patterns

We used the methods of Woodward et al. (1984) for developing gradients to evaluate nest spacing patterns. Seventy-three and 34 quadrats, 37 ha in size, were enscribed on photographs of Orange Lake and Lake Woodruff, respectively. Nest locations and corresponding status plotted during aerial surveys were transcribed onto maps containing the quadrats. This procedure was repeated for nesting data from 1983 to 1985 on Orange Lake and Lake Woodruff. Other nesting data (1980–1982) for Orange Lake were obtained from the Florida Game and Fresh Water Fish Commission.

Data Analysis

Between-year data were tested for similar distributions within both study areas using the F-statistic (Snedecor and Cochran 1976). To test if the combined data were sampled from a multivariate normal population, probability plots based on the Kolmogorov D-statistic were developed. Skewed distributions of percent shade required transformation using the arcsin square root; water distance and height were transformed using the square root of those values (Sokal and Rohlf 1981). To avoid biases related to normality assumptions, logistic regression (Afifi and Clark 1984) was used to develop logistic multiple regression models for predicting nest fate.

Nest spacing patterns were analyzed using Morisita's Index (I_m) of Aggregation (Morisita 1959). If $I_m = 1$, dispersion of nests was random; if >1, nests were aggregated; and if <1, nests had a uniform pattern. Significance of the deviation of I_m from 1 was tested by the F-statistic ($P = 0.05$). Distribution of depredated nests was tested using the same procedure. Year to year variation in the distribution of these spacing patterns was examined using Spearman rank correlation coefficients.

Results

Habitat Variables

Status of successful and depredated nests was determined for 146 alligator nests on Orange Lake and 54 nests on Lake Woodruff. Because neither the variation in rate of nest success nor rate of nest depredation differed ($P > 0.05$) between 1984 and 1985 at either Orange Lake ($F = 1.19$, df = 79,67) or Lake Woodruff ($F = 1.13$, df = 29,26), data were pooled.

Shore distance was retained as the only significant variable in the logistic regression model developed for Orange Lake (Table 1); however, the low coefficient of determination indicates limited usefulness. Vegetation density, nest shade, substrate height, and water distance were not included. No variables were retained by the logistic regression procedure for Lake Woodruff data (Table 1). Rejection of variables in their order of decreasing value was: water distance, shore distance, nest shade, vegetation density, and height.

Table 1. Logistic regression analyses of 5 habitat variables associated with alligator nests on Orange Lake and Lake Woodruff, Florida, 1984–1985.

Variable	Orange Lake (N = 146 nests)			Lake Woodruff (N = 54 nests)		
	$\bar{X}^2$	P	r^2	$\bar{X}^2$	P	r^2
Shade	0.10	0.77	0.00	0.10	0.75	0.00
Height	0.02	0.88	0.00	0.02	0.90	0.00
Vegetation density	0.62	0.43	0.00	0.06	0.80	0.00
Shore distance	4.61	0.03	0.01	0.15	0.69	0.00
Water distance	0.02	0.90	0.00	3.31	0.07	0.14

Table 2. Morisita's Index of Aggregation and associated F-statistics for the 1980–1985 nesting seasons, Orange Lake, Florida.

Year	Number of nests[a]	Index value (I_m)	F value
		All nests	
1980	77	1.77	1.87[b]
1981	66	1.33	1.16
1982	78	1.62	1.60[b]
1983	94	1.21	1.31
1984	86	1.32	1.48[b]
1985	86	1.26	1.27
		Depredated nests	
1980	34	1.33	1.16
1981	41	0.99	1.00
1982	32	2.88	1.87[b]
1983	52	1.20	1.18
1984	46	1.38	1.26
1985	42	1.67	1.40[b]

[a]Based on 68 quadrants in all years.
[b]Significantly >1, indicating clumped distribution (P <0.05).

Nest Spacing Patterns

Spacing patterns of all nests considered on Orange Lake were clumped in 1980, 1982, and 1984, and spacing patterns of depredated nests were clumped in 1982 and 1984 (Table 2). Even in years when total nest distributions were clumped, correlation coefficients were weak, indicating that reuse of specific quadrats for nesting did not occur from year to year. Similarly, low correlation was obtained for among-year comparisons of depredated nests, suggesting that depredation did not occur in the same areas annually. Depredated nests were clumped only in 1984 on Lake Woodruff, precluding any attempts to analyze between-year correlations.

Discussion

The prediction of nest depredation, measured by aerial survey, was independent of 5 habitat variables: (1) nest shade, (2) height of the nesting substrate, (3) vegetation density, (4) distance of the nest to the nearest permanent shoreline, and

(5) distance of the nest to the nearest open water. The inability to predict nest predation is likely the result of highly variable relationships between nest predation and the habitat variables. Webb et al. (1983) argued that models developed to predict flood induced losses of estuarine crocodile (*Crocodylus porosus*) nests (Magnusson et al. 1978) were unable to account for the variability in habitat variables. Furthermore, subjective estimations of the habitat variables also may have contributed to the ineffectual estimation of nest status.

In this study, nest shade and distance of the nest to open water were initially thought to represent habitat conditions that would provide nesting females with thermoregulatory refuge while attending nest sites. That nest shade was not a reliable predictor of nest fate may be partially explained by the fact that female alligators probably spend little time on the nest during daylight hours (Joanen 1969). This is not unexpected because the threat of nest depredation is greatest during the crepuscular and nocturnal foraging periods of raccoons (Mech et al. 1966). Lack of female attendance during surveys was particularly noticeable on Lake Woodruff, where the majority of nests were located in open sand cordgrass marsh. Although aerial estimations of nest shade and distance of the nest to open water were not statistically useful, proximity to refugia would still be an energetic advantage and allow attendance for a greater time during incubation. Because females invest in nest guarding, measures to alleviate the cost of that investment may be a reproductive advantage. The interpretation of these habitat variables is also confounded because although trees provided shade, they also supplied a substrate support on which nests were constructed. Therefore, females may construct nests in shaded areas not to satisfy thermoregulatory requirements but for the support provided the nest (i.e., flooding is a competing risk with depredation in some wetlands).

Graham (1981) and Webb et al. (1983) identified proximity of deep permanent water and the presence of wallows as potential deepwater refugia for nesting estuarine crocodiles. In this study, wallows were not always distinguishable during aerial survey; dense vegetation and multiple access points often obscured their presence. Therefore, the actual distance of nests to open water was probably less than estimated from aerial survey.

Interpretation of substrate height was confounded by changing water levels and vegetation densities. Originally, substrate height was perceived as a subjective estimation of the relative use by foraging raccoons of wet vs. dry habitats. Dry areas, such as dikes or shore margins, were thought to represent corridors frequented by raccoons (Urban 1970). However, in this study, dikes were heavily vegetated and may deter raccoon movement, while shore margins generally were open and appeared more accessible to raccoons. This type of confounding relationship could not be isolated in the model building process. Also, estimates of substrate height were not consistent on Orange Lake and Lake Woodruff due to rising water levels throughout incubation during 1985. The inconsistency of substrate height as a discrete variable indicates that it provides little useful information when subjectively estimated.

Distance from the nest to the nearest permanent shoreline was first tested as a potential predictor of nest fate by Deitz and Hines (1980). They reasoned that nests close to a treeline would be subject to greater depredation than nests located deep in the marsh. However, they found no difference in hatching success between nests classified as fringe, or deep marsh nests.

Results from Orange Lake indicated that although spacing of all alligator nests was clumped during 1980, 1982, and 1984, there was low correlation between years; thus, the reuse of specific quadrats by nesting females appeared limited. Furthermore, the distribution of depredated nests appeared independent of total nest spacing. Clumping of depredated nests and total nests occurred only in 1982. More importantly, only a weak relationship was detected between depredation patterns in 1982 and 1985, when raccoon depredation was aggregated on Orange Lake. Consequently, if nest depredation is clumped and independent of total nest spacing, it is not spacially consistent from year to year.

Further, nest depredation on Orange Lake was clumped only during periods of low water. This relationship implies that raccoon foraging strategies are influenced by water height. Cagle (1949) speculated that water level changes affected the availability of specific food items and caused shifts in foods consumed by raccoons. Therefore, under conditions of low water, foods such as mollusks (*Anodonata* spp., *Campeloma* spp., *Pomacea* spp.) and crayfish (*Procambarus* spp.) may be locally abundant, resulting in reduced foraging ranges by raccoons. If alligator nests were present in these intensely foraged areas, a greater proportion of them likely would be depredated. However, that aggregations of depredated nests did not occur in the same areas during similar drought conditions (1982 and 1985) suggests that shifts or changes in food type and abundance probably influence where raccoons will forage.

Conclusion

Although results of this study did not identify any habitat variables or nest spacing patterns suitable for developing predictive models, it is possible that alternative uses of the 5 habitat variables could lead to more robust models. Jacobsen and Kushlan (1986) and Webb et al. (1983) developed models that could predict nest fate of American alligators and estuarine crocodiles where flooding was the decimating factor. However, development of these models required ground inspections and precise measurements of water level and clutch heights over many years.

Although costly, ranching demographically "free" nests is a concept that should be pursued further. Until prediction of nest fate is possible, management programs should target the most accessible nests, thereby reducing costs. Future research efforts should: (1) determine whether success of accessible nests is equal to that of inaccessible nests, (2) monitor the occurrence of depredated nest clumping during a longer period, (3) examine raccoon densities, movement, and behavior in wetland systems where alligator nest depredation is important, and (4) incorporate a more precise measure of hydrological data when evaluating depredation patterns.

Literature Cited

Afifi, A. A. and V. Clark. 1984. Computer-aided multivariate analysis. Wadsworth, Inc., London. 458pp.

Cagle, F. R. 1949. Notes on the raccoon, *Procyon lotor magalodous* Lowery. J. Mammal. 30:45–47.

Cowardin, L. M., V. Carter, F. G. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Dep. Int., Fish and Wildl. Serv. FWS/OBS–79.31. 103pp.

Deitz, D. C. and T. C. Hines. 1980. Alligator nesting in north-central Florida. Copeia 32:249–258.

Fleming, D. M., A. W. Palmisano, and T. Joanen. 1976. Food habits of coastal marsh raccoons with observations of alligator nest predation. Proc. Annu. Conf. Southeast. Assoc. Game and Fish Comm. 30:348–357.

Goodwin, T. M. and W. R. Marion. 1978. Aspects of the nesting ecology of American alligators (*Alligator mississippiensis*) in north-central Florida. Herpetologica 34:43–47.

Graham, A. 1981. Mapping the pattern of crocodilc nesting activity in Papua New Guinea. Papua New Guinea Dep. Lands Environ., Wildl. Div., Field Doc. 3. 50pp.

Hayes, R. L., C. Summers, and W. Seitz. 1981. Estimating wildlife habitat variables. U.S. Dep. Int., Fish and Wildl. Serv. FWS/OBS–81/47. 111pp.

Hines, T. C., C. L. Abercrombie, H. F. Percival, and A. R. Woodward. 1986. Florida alligator economics harvest and conservation. Pages 132–142 *in* S. Gorzula, ed. Crocodiles. Internat. Union Conserv. Nat., Caracas, Venezuela.

——— and H. F. Percival. 1987. Alligator management and value-added-conservation in Florida. Pages 164–173 *in* D. J. Decker and G. R. Goff, eds. Valuing wildlife resources: economic and social perspectives. Westview Press, Boulder.

Jacobsen, T. and J. A. Kushlan. 1986. Alligator nest flooding in the southern Everglades: A methodology for management. Pages 153–166 *in* S. Gorzula, ed. Crocodiles. Internat. Union Conserv. Nat., Caracas, Venezuela.

Joanen, T. 1969. Nesting ecology of alligators in Louisiana. Proc. Annu. Conf. Southeast. Assoc. Game and Fish Comm. 23:141–151.

Magnusson, W. E., G. C. Grigg, and J. A. Taylor. 1978. An aerial survey of potential nesting areas of the saltwater crocodile, *Crocodylus porosus* Schneider, on the north coast of Arnhem Land, northern Australia. Australian Wildl. Res. 5:401–415.

Mech, L. D., J. R. Tester, and D. W. Warner. 1966. Fall daytime resting habits of raccoons as determined by telemetry. J. Mammal. 47:450–466.

Metzen, W. D. 1977. Nesting ecology of alligators on the Okefenokee National Wildlife Refuge. Proc. Annu. Conf. Southeast. Assoc. Game and Fish Comm. 31:29–32.

Morisita, M. 1959. Measuring the dispersion of individuals and analysis of distributional patterns. Memoirs Faculty Science Kyushu University Series E Biology 2:215–235.

National Research Council 1983. Crocodiles as a resource for the tropics. Natl. Acad. Press. Washington, D.C. 59pp.

Rose, M. 1982. Crocodile management and husbandry in Papua New Guinea. Pages 148–163 *in* Crocodiles. Internat. Union Conserv. Nat., Victoria Falls, Zimbabwe and St. Lucia Estuary, South Africa.

Snedecor, G. W. and W. G. Cochran. 1976. Statistical methods. Univ. of Iowa Press, Ames. 593pp.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Co., New York. 859pp.
Urban, C. 1970. Raccoon populations, movement patterns, and predation on a managed waterfowl marsh. J. Wildl. Manage. 34:372–382.
Webb, G. J. W., G. C. Sack, R. Buckworth, and S. C. Manolis. 1983. An examination of *Crocodylus porosus* nests in two northern Australian freshwater swamps, with an analysis of embryo mortality. Australian Wildl. Res. 10:571–605.
Wilkinson, P. M. 1983. Nesting ecology of the American alligator in coastal South Carolina. S.C. Wildl. and Marine Resour. Dep. Completion Rep., Charleston. 113pp.
Wood, J. M., A. R. Woodward, S. R. Humphrey, and T. C. Hines. 1985. Night counts as an index of American alligator population trends. Wildl. Soc. Bul. 13:262–272.
Woodward, A. R., T. C. Hines, C. L. Abercrombie, and C. Hope. 1984. Spacing patterns in alligator nests. J. Herpetol. 18:8–12.