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Alligator Nesting in North-Central Florida

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A sample of 111 *Alligator mississippiensis* nests from Orange and Lochloosa lakes and Payne's Prairie in northern Florida was examined. Nest construction and egg deposition occurred from early June to mid-July, similar to dates reported for Louisiana. The minimum construction period averaged 10.7 ± 4.3 days. Sawgrass, *Cladium jamaicensis,* was preferred for nest construction on Orange and Lochloosa lakes. The number of eggs per clutch for Payne's Prairie averaged 38.7 ± 7.0 during 1974–1977; the average for Orange-Lochloosa was 36.1 ± 9.1 in 1975–1977. The two study areas were not significantly different with respect to number of eggs/clutch, mean clutch weight or mean egg weight. Variation in egg size between clutches was considerable, and was comparable to data available for other crocodilians. The majority of nests in both study areas were preyed upon by raccoons; nests opened by the investigators were depredated twice as often as undisturbed nests in both areas. Females consistently attended or defended 14.9% of the Payne's Prairie nests, while no defense or consistent attendance was observed on Orange or Lochloosa lakes. Hatching success was 35.5% for all nests, and 67.9% for nests not opened by investigators. All successful nests were apparently opened by the parent. At least 50.6% of the eggs in 12 successful nests produced young which reached the water. Changes in alligator nesting behavior throughout the southeastern U.S. in relation to the history of human disturbance are discussed.

RESEARCH on the American alligator, *Alligator mississippiensis,* has increased recently, due in part to the "endangered" classification of some populations and the consequent need for information relevant to their management. Recent studies have indicated that American alligators (along with other crocodilians) have complex social behavior (Garrick and Lang, 1977; Garrick et al., 1978) and that they also may have significant impacts on marsh ecosystems (Kushlan, 1974). Their reproductive ecology is particularly interesting in that it involves a degree of parental care not found in noncrocodilian reptiles (Cott, 1971), and also

because it is implicit in the rapid recovery which some reduced populations have shown following protection.

McIlhenny (1935) provided detailed information on female behavior during nest construction, egg laying and incubation, but the first quantitative study was Joanen's (1969) in Louisiana's coastal marsh. He examined 315 nests over a 5-year period and considered such factors as the timing and temperature of incubation, female visitation, attendance at the nest and predation patterns. Studies by Fogarty (1974) and Ogden (1976) examined nesting ecology in the Everglades environment of southern Florida, and more recent work by Metzen (1977) provided comparable data from Okefenokee Swamp, Georgia. None of these studies involved as many nests or were as comprehensive as Joanen (1969).

In north-central Florida *A. mississippiensis* occupies virtually all wetland habitats. These include the large shallow lakes characteristic of the region where populations may reach densities of 43.5 alligators/km of lake shoreline, the highest recorded from within the animal's range. Our study of nesting in north-central Florida was initiated in 1974 to allow comparisons with other regions, to provide additional information on population dynamics and to determine some of the factors affecting nesting success in different habitat types.

STUDY AREAS

Nests were located on Payne's Prairie State Preserve and on Orange and Lochloosa lakes, Alachua County, Florida. Payne's Prairie is a 5,036 hectare marshy basin, typical of Florida wet prairie habitat except that drainage canals and levees have been constructed throughout the basin. White (1974) presented data on the hydrology and vegetation of the area. Dominant plant species in areas where alligator nesting occurs include *Pontedaria lanceolata*, *Jussiaea peruviana*, *Typha* sp., *Salix carolinensis*, *Panicum hematomon*, *Juncus effusus* and *Hydrocotyle umbellata* (White, 1974). Orange and Lochloosa lakes have extensive marshy areas covering portions of both lake basins. Most alligator nesting took place in these marshy areas, although some nests were located in the fringe around the open water portions of the lakes. Characteristic of these marsh areas and portions of the fringe as well is a heavy build-up of peat resulting in floating islands. Vegetational composition of

these islands and fringe areas is largely *Sagittaria lancifolia*, *Cladium jamaicensis*, *Hydrocotyle umbellata*, *Myrica cerifera*, *Cephalanthus occidentalis* and *Decodon verticillatus*.

The climate of north-central Florida is humid-subtropical. Mean minimum and maximum air temperatures range from 8.3–20.3 C in January to 21.8–32.7 C in August (data from the University of Florida Agricultural Experiment Station, Gainesville, Florida). Annual rainfall averages 140 cm, of which 53% (73 cm) falls between 1 June and 30 September.

METHODS

Most of the nests on Payne's Prairie were located by searching levees on foot. Aerial searches were used to locate a limited number of nests in the marsh, although these were not monitored closely since the area was closed to marsh vehicles. Some nests on Payne's Prairie were visited regularly throughout the construction period to obtain information on construction and egg deposition dates. Aerial searches on Orange and Lochloosa lakes were conducted in late June and early July, when most nests were complete. Nest measurements, clutch counts, and other pertinent data were taken after eggs were laid. We normally did not disturb the nests except to take occasional nest temperatures. Nests were then visited at least semi-weekly. Almost all such visits were in daylight.

High predation rates on nests which we opened in 1974 and 1975 suggested that our manipulations might adversely affect nest success. In 1976 and 1977, 46 nests on Orange Lake and 23 nests on Payne's Prairie were randomly designated "open" or "unopened." "Open" nests were opened from the top, and the eggs were removed, counted, and sometimes weighed (without rolling) before being replaced; the nest was then re-covered and packed. Initial visits to "unopened" nests did not involve any physical contact with the nest. On subsequent visits, "open" and "unopened" nests were treated identically—i.e., nests were approached only closely enough to determine their condition. Nests were visited on this basis until hatching or until they were destroyed.

RESULTS

Nest construction.—Periods of nest construction and egg deposition are shown in Fig. 1 which suggests a positive relationship between timing
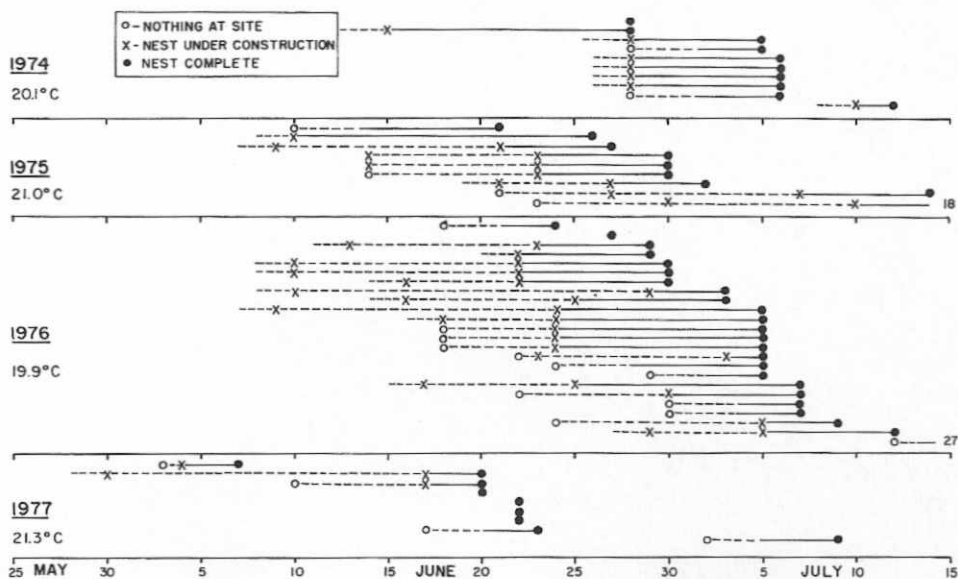
Fig. 1. Construction dates for Payne's Prairie alligator nests. Mean minimum June air temperatures appear at left. The solid bars indicate periods during which eggs were laid; dotted lines indicate periods of nest construction.

of nesting and mean minimum June air temperatures, similar to that reported by Joanen (1969) and Joanen and McNease (1978). Peak nesting occurred during the third week in June, corresponding to dates observed in Louisiana. The earliest start of nest construction was 30 May and the latest between 12 and 27 July. The earliest egg deposition date was 4–7 June 1977 and the latest was 12–27 July 1976.

As McIlhenny (1935) and subsequent workers noted, construction of the nest mound by female *A. mississippiensis* was a complex process, involving many trips to the nest site to gather and shape nest material. The minimum construction period for 18 nests on Payne's Prairie averaged 10.7 ± 4.3 days (mean ± standard deviation, range 2–20 days). This sample was slightly biased, since we were unable to determine accurate minimum construction periods for 6 nests which were constructed in 7 days or less.

No females were observed in the process of building a nest. Checks made during construction periods indicated that most, if not all, of this work took place at night. Several nights of no activity were sometimes interspersed between nights on which material was added or reshaped. Carr (1976) reported that one female visited her nest on 8 nights between the start of

construction on 3 June and egg deposition on 21 June, and failed to visit it on 10 nights. Construction was occasionally quite rapid—one nest in 1977 was completed in less than 84 hours. In six cases (5.4% of 111 nests) the initial site was abandoned after a mound had been constructed and a second mound was built in which eggs were eventually deposited. Joanen (1969) and Fogarty (1974) also reported false nesting in *A. mississippiensis*.

Nests on Payne's Prairie were located in both shaded and unshaded situations. Levees were heavily utilized where available and marsh nests were rarely seen within 200 m of a levee, suggesting that levees were actively sought. Materials used in nesting reflected the plant species composition in the immediate vicinity of the nest. At the Orange-Lochloosa area there was a definite preference for sawgrass, *Cladium jamaicensis,* a species absent on Payne's Prairie. Eighty-one percent of all nests on Orange-Lochloosa were located in and constructed primarily of *Cladium* which was estimated not to exceed 25% of the ground cover in nesting areas. Sawgrass clumps on Orange-Lochloosa grew in a circular pattern, with an accumulation of old culms in the center. These dead stems provided abundant nesting material, and rhizome build-up in the clump provided a solid
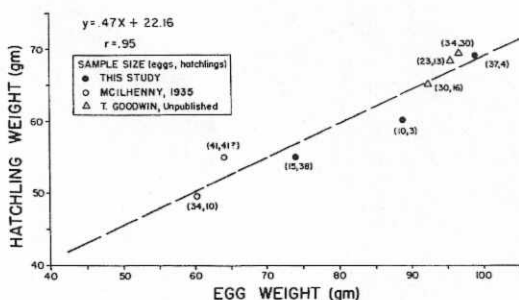
Fig. 2. Relationship between mean egg weight and mean hatchling weight.

Fig. 3. Relationship between number of eggs per clutch and mean egg weight.

foundation under the nest. Twelve nests on Orange Lake had a mean height of 73.7 ± 12.9 cm (range 60–105 cm), significantly higher ($P <$ 0.01, t-test) than the mean height of 49 ± 12.9 cm (range 25–75 cm) for 36 nests on Payne's Prairie where *Cladium* was not available. The density of sawgrass stands also appeared to provide better concealment for the nests than most other available locations.

Clutch size.—There were no significant differences between the two study areas or between years with respect to number of eggs per clutch, mean clutch weight, or mean egg weight ($P <$ 0.05, analysis of variance; Tables 1, 2). The range of egg weights between clutches was considerable, with the largest mean per clutch (99.3 g) nearly twice as large as the smallest (54.0 g). Egg weight was found to correlate positively with hatchling weight (Fig. 2). Variation in egg weight within a clutch was quite small; standard errors were usually < 0.5 g and always < 1 g. There was a positive relationship between mean egg weight and number of eggs per clutch (Fig. 3). Although significant, the correlation was not strong (r = 0.49, $P < .05$). The variation in mean egg weight was quite large for clutches of 30 to 45 eggs.
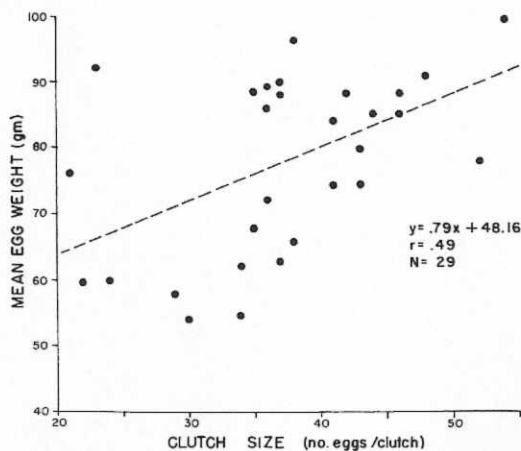
Females normally were not present at nests when we examined them; consequently, we have few data on female size. There was no significant relationship between number of eggs per clutch and total length of the female (n = 14), as also found by Joanen (1969) in Louisiana. Both mean egg weight and total clutch weight increased with female size, although neither relationship was significant at the .05 level; this may reflect our small sample size (n = 7; not all clutches were weighed). The smallest female observed with a nest was not captured, but her total length was estimated to be approximately 1.7 m. This animal produced eggs which averaged 54.0 g, the smallest we observed.

Most *A. mississippiensis* eggs examined during the first two weeks of incubation had a conspicuous white opaque band approximately 25 mm wide located transversely around the center. This was also reported by Clarke (1891, Figs. 1, 5, 7), who suggested that the opacity

TABLE 1. CLUTCH SIZES FOR NORTH FLORIDA ALLIGATOR NESTS. ($\bar{x}$ ± s.d.)

	Payne's Prairie			Orange-Lochloosa		
Year	N	Mean clutch	Range	N	Mean clutch	Range
1974	3	31.3	23–41			
1975	9	41.4 ± 3.1	38–46	3	39.3	36–45
1976	19	38.9 ± 8.1	24–53	11	35.9 ± 7.8	22–47
1977	6	37.8 ± 5.0	30–43	16	35.6 ± 10.4	21–54
Total	37	38.7 ± 7.0	23–53	30	36.1 ± 9.1	21–54

TABLE 2. TOTAL CLUTCH AND EGG WEIGHTS FOR NORTH FLORIDA ALLIGATOR NESTS, 1976–77: ($\bar{x}$ ± s.d.)

	Payne's Prairie (N = 17)	Orange-Lochloosa (N = 12)	Combined (N = 29)
Total clutch weight (g)	2,859 ± 856	3,069 ± 1,189	2,946 ± 992
Range	1,432–4,053	1,311–5,362	1,311–5,362
Egg weight (g)	75.4 ± 14.0	80.4 ± 12.7	77.5 ± 13.5
Range	54.0–96.6	59.6–99.3	54.0–99.3

resulted from rapid changes in the underlying shell membrane associated with increased gas exchange by the developing embyro. Eggs without such a band appeared somewhat translucent. Fourteen banded and 12 unbanded eggs were removed from one nest and candled; there was no evidence of development in any unbanded eggs, while opaque regions (assumed to overlie a developing embryo) were present in the entire banded sample. These eggs were artificially incubated at 29 C and recandled after 10 days with identical results; excessive mold growth terminated the experiment shortly thereafter. Additional unbanded eggs candled in the field also showed no development. We therefore considered all unbanded eggs to be infertile, although early arrested development might produce similar results and make this a slight overestimate of infertility. Using this criterion, the mean infertility per clutch for 29 clutches was 10.9 ± 17.3% (range 0–77%); 10.6% of all eggs (n = 1,072) from these clutches were infertile.

Nest temperatures.—Egg cavity temperatures were taken during daylight hours at 24 nests, most of which were unshaded; the mean of 63 determinations was 30.7 ± 1.6 C (range 27.5–34 C). Air temperatures taken simultaneously averaged 29.8 ± 2.8 C (range 24–36 C), while nest surface temperatures for unshaded nests reached 48 C. The relative constancy of egg cavity temperature when compared with fluctuations in air and surface temperatures has been documented by Chabreck (1973) for *A. mississippiensis* and by Webb et al. (1977) for *Crocodylus porosus* nests.

Hatching success.—Predators destroyed all eggs in the majority of nests from both study areas

TABLE 3. NESTING SUCCESS OF NORTH FLORIDA ALLIGATORS. Nests in the "hatched" category produced at least one living young; the nest in the "other" category was apparently destroyed by the parent during maintenance.

Year	N	Hatched	Depredated	Flooded	Artificially hatched	No determination	Other
Payne's Prairie							
1974	8	1	6	1			
1975	9	2	3	2	1	1	
1976	22	6	14			2	
1977	8	4	4				
Total	47	13	27	3	1	3	
%		30.2*	62.8*	6.8*			
Orange Lake							
1975	3	2	1				
1976	18	7	10				1
1977	32	16	16				
Total	53	25	27				1
%		47.2%	50.9%				1.9%

* Percentages calculated on the basis of 43 nests for which final determinations were made.

TABLE 4. FEMALE ATTENDANCE AT PAYNE'S PRAIRIE REMOTE NESTS.

	Female in attendance		No female in attendance	
	N	Hatched	N	Hatched
Opened	5	4 (80%)	22	2 (9.1%)
Not opened	2	1 (50%)	14	6 (42.9%)
Overall	7	5 (71.5%)	36	8 (22.2%)

Chi-square significant, $P < .05$.

(Table 3). Raccoons, *Procyon lotor*, were positively identified or suspected of being responsible in 85% (46 of 64) of these cases, while otters, *Lutra canadensis*, were suspected in 7% (4 of 54) of the remainder. Flooding was not a major factor and accounted for only 3 losses.

Pooled data from 1976 and 1977 confirmed the hypothesis that manipulations at the nest site increased predation. On Payne's Prairie, only 2 of 7 "unopened" nests (28.6%) versus 15 of 16 "open" nests (93.8%) were destroyed by predators ($P = 0.003$, Fisher exact probability test); on Orange Lake, 7 of 21 "unopened" nests (33.3%) versus 17 of 25 "open" nests (68.0%) were destroyed ($P < .01$, Chi-square test). A similar increase in predation was noted when general human disturbance around the nest was great. On Payne's Prairie, 13 of 47 nests in areas without vehicular traffic or human visitation hatched (Table 3), while only 1 of an additional 11 nests examined in areas with heavy traffic hatched ($P = .01$, Fisher exact probability test).

Based on raccoon foraging patterns, we hypothesized that nests located along the fringe of Orange Lake and therefore closer to the treeline would be subject to higher predation than nests deep in the marsh. We subdivided our sample of nests from 1976–1977 into fringe and marsh categories (within "open" and "unopened" treatments) based on proximity to the treeline, but found no significant difference in hatching success between these categories ($P > .05$, analysis of variance); there were also no significant interactions with effects of the open/unopened treatments.

Alligator nest mounds were used extensively by nesting turtles, especially *Trionyx ferox* and *Chrysemys nelsoni* (Goodwin and Marion, 1977); 16 clutches representing at least 216 eggs were counted in one nest mound (Deitz and Jackson, in press). In many instances of predation, the base of the alligator nest was excavated and the turtle eggs removed first. Several days sometimes elapsed between these initial excavations and the first disturbance of the alligator egg cavity. The appearance of the scattered material, along with eggshell fragments, in a raccoon-depredated nest indicated that mounds were also thoroughly searched for turtle eggs after the alligator eggs had been eaten.

Female attendance.—It was difficult to quantify female attendance at the nest site, since there was often evidence of regular visitation at nests (e.g. tracks, fresh nest material, enlargement of trails or pools near nest) where females were never observed. Fresh material and tail drags across nests were more common during the first three to four weeks of incubation, which agreed with Joanen's (1969) results from Louisiana. Aggressive defense of the nest was observed at five sites on Payne's Prairie from 1974–1977, and probably involved four different alligators. At seven other nests, alligators (assumed to be females) were present whenever the nest was visited and remained visible near the nest when obviously aware of our presence (as indicated by head movements and other postural adjustments). These animals did not hiss, inflate their bodies, or make any other threatening movements. The above 12 nests were scored as positive for female attendance, since we believed that they received care of a different quality than nests at which females were occasionally or never seen. No nests on Orange Lake were scored as positive.

Seven of 47 nests (14.9%) in remote areas on Payne's Prairie were scored as positive and the eggs in five of these seven (71.4%) hatched (Table 4). Hatching success for undefended nests was significantly lower ($P < .05$, Chi-square test). Four of five remote nests on Payne's Prairie which we opened, and which were attended by females, hatched, despite the extremely high predation rate for other opened nests (Table 3). Defending females also were present more consistently at the nest than were other females; one female was present on 19 of 20 visits to her nest in 1974.

Hatching.—All of the nests in our study which hatched were extensively excavated on one side and it appeared that all had been opened by the female. Most appeared as in Fig. 4—an excavation from the top center down to the bottom of the egg cavity, semi-circular when

viewed from above and sloping broadly out and down to the side. The opening usually faced one of the female's trails to the nest. The open side of the nest was frequently flattened into a ramp, probably by the body of the female as she moved up the nest to the egg cavity.

At least 50.6% of the eggs in 12 successful nests eventually produced young that reached the water. Infertile, rotten, or unhatched eggs were almost never present in a hatched nest; we assumed that they were removed by the female while releasing young and possibly swallowed [also reported for *Crocodylus niloticus* (Pooley, 1977)]. On two occasions, we found unhatched living embryos in nests that had already been opened by the female. These animals eventually died in the nest.

Hatchlings remained in the vicinity of the nest for periods ranging from 72 hours to several weeks. They usually could be located in a wallow or widened alligator trail used by the female. Female attendance and defence of the pod was correlated with the behavior at the nest site, i.e., females which aggressively defended their nests against humans also defended their young.

Fig. 4. Photograph of an alligator nest immediately after hatching. The female's activity has compressed the material on the right into a ramp.

DISCUSSION

Egg production is clearly one of many possible important influences on crocodilian population density. The average number of eggs per clutch for our sample (37.5 ± 8.1, both localities combined) is comparable with that found in Louisiana (38.9—Joanen, 1969), but higher than means reported for the Everglades (33.1—Fogarty, 1974) or the Okefenokee (30—Metzen, 1977). Similarly, population densities of *A. mississippiensis* in Orange Lake and other north and central Florida lake systems appear equal to those found in the Louisiana coastal marshes, but are greater than populations in the Everglades. However, the wide variation in rates of nest predation also reported for these areas indicates that variation in egg number alone probably does not have a significant effect on population density.

Considerable variation in mean egg weight between clutches has been documented for 3 other species of crocodilians: *Caiman crocodilus* (Staton and Dixon, 1977), *Crocodylus palustris* (Deraniyagala, 1953) and *Crocodylus porosus* (Webb et al., 1977). In none of these species is there a correlation between number of eggs per clutch and mean egg weight. The absence of

such a relationship also was implied by Cott (1961:275) for *Crocodylus niloticus*. This variation in mean egg weight may explain the absence of any significant relationship between egg number and female size in *A. mississippiensis* and suggests that for all crocodilians total clutch weight may be better correlated with size than egg number.

Egg size may be regulated by ontogenetic and/or environmental factors. Mean egg weights for the first clutches produced by one *A. mississippiensis* examined by McIlhenny (1935:106) and two by Joanen and McNease (1975) were 60, 59 and 63 g, respectively—substantially below our mean of 77.5 g. Evidence presented here for *A. mississippiensis* (Fig. 3) and by Staton and Dixon (1977) for *Caiman crocodilus* suggests that under different circumstances females might produce either many small young or fewer, larger young with the same total clutch weight. A total clutch weight of 2,946 g (the mean in our study) would produce from 30 of the largest to 54 of the smallest hatchlings we observed. Staton and Dixon (1977) also published data for *C. crocodilus* which demonstrated a decline in mean egg weight during the three-month laying season. *Caiman* which hatched early in the subsequent dry season were thus larger than those which hatched later. They presumed that larger young were selected on the basis of reduced mortality over a longer dry period. We are presently attempting to determine the effects of hatchling size on mortality in *A. mississippiensis*.

Raccoon predation was the only significant factor affecting hatching success in our study. Raccoons were also the major predators of al-

ligator nests in Louisiana (Joanen, 1969; Fleming et al., 1976) and of *Crocodylus acutus* nests in south Florida (Ogden, 1978), although these studies also reported substantial flooding losses. We presume that the increase in predation due to our interference involved an increase in olfactory cues available to raccoons; odors which were normally confined to the egg cavity were possibly released by our opening the nest and inevitably rearranging some of the material. We predict that manipulations of other crocodilian nests visited by olfactorily-oriented predators (such as varanid lizards) should also increase predation. The rate of predation which we recorded for unopened nests, 43% of 35 nests over 4 years, was higher than that reported for alligators anywhere except the Okefenokee, where Metzen (1977) recorded an 86% predation rate due primarily to black bears. This may be due partly to the extensive usage of our nests by turtles, which may have provided additional olfactory cues.

The consistent female attendance which we observed at some nests may have a significant effect on hatching success when predation is likely, such as our opened nests on Payne's Prairie. Carr (1976) reports one defensive female present at 25 of 25 and 28 of 28 visits to her nest in two different years. We do not regard such nests as having the same susceptibility to raccoon predation as those where the female is seldom present. Metzen (1977) observed significantly lower rates of black bear predation on defended nests in the Okefenokee. Consistent female attendance may also result in better nest maintenance. Both attended and unattended nests often had material added to them during the first 3 weeks of incubation, and one nest was repaired during the 9th week after raccoons had exposed the egg cavity and eaten several eggs. Nest repair following predation also was reported for *Caiman crocodilus* (Staton and Dixon, 1977). The packed and irregularly coned shape of a well-maintained nest may be important in shedding water during the frequent summer thunderstorms; two nests which received little or no care during incubation were eventually preyed on after heavy rains had exposed the egg cavity. Telemetry studies have indicated that most females remain in the general vicinity of their nest throughout incubation even when there is no consistent close attendance or defense of the site (Joanen and McNease, 1970; Goodwin, 1977).

Most investigations of *A. mississippiensis* nest-

ing behavior have reported on female nest defense against humans (McIlhenny, 1935; Joanen, 1969; Metzen, 1977). While this is usually the only criterion available to assess tenacity of defense, it is probably inadequate as a reliable measure of female anti-predator behavior. We have assumed that female *A. mississippiensis* which threaten or lunge at humans will also drive off raccoons. It is surely unreasonable to make the converse assumption, i.e., that alligators which do not threaten humans will also not threaten raccoons. Humans may be reasonable facsimiles of large predators such as bears, which evidently were significant nest predators when they were more abundant in Florida (Reese, 1915). Frequency of anti-human defensive behavior may therefore not be entirely irrelevant, as Kushlan and Kushlan (1979) also argue. However, alligators may be fearful of humans for a variety of reasons which would not necessarily affect guarding behavior against smaller nest predators. On one occasion during this study, an alligator which had not threatened humans was observed to threaten and drive off a raccoon.

The use of motor vehicles, such as the airboats and marsh buggies necessary to most alligator nesting investigations, probably results in underestimates of frequencies of attendance or defense, particularly in areas where there is a history of harassment by humans using such vehicles. Airboat usage for frogging, and until recently for alligator hunting, is common on Orange-Lochloosa. It was unfortunately essential for our study there, during which we observed no female nest attendance. We did observe alligators attending nests when aerial surveys were conducted, suggesting that the animals were fearful of us or our vehicles; the airboat was not used on Payne's Prairie where a 14.9% attendance rate was recorded.

Some evidence suggests that alligators may also become habituated to humans. Five of eleven nests (45.4%) on Payne's Prairie in areas with frequent human visitation but no alligator harassment during or for at least 5 years prior to the study were consistently attended or defended. This is much higher than the 14.9% attendance we recorded for remote areas. Kushlan and Kushlan (in press) found a higher frequency of nest defense for a similar situation in Everglades National Park.

The effects of recent intense hunting on nest-guarding in *A. mississippiensis* are particularly difficult to assess. Populations on state or fed-

eral refuges (where most investigations of nesting behavior are conducted) should have been less influenced than others, assuming that negative encounters with humans were fewer. Nest defense frequencies (against humans) from refuges across the Southeast are consistently low: Rockefeller Refuge, Louisiana—9.2% (Joanen, 1969); Okefenokee Swamp, Georgia—18.7% (Metzen, 1977); Payne's Prairie, Florida—14.9% (this study); and Everglades National Park, Florida—22% (Kushlan and Kushlan, 1979). If our experience with Orange-Lochloosa is any indication, this segment of the population also will abandon defensive behavior when harassed. Interestingly, J. Schortemeyer (pers. comm.) believes that the incidence of female defensive behavior in the Everglades is increasing. He attributes this to recruitment of young females to the breeding population; due to recent protection, these young animals may not have been harassed as much as older alligators and consequently may be more likely to defend nests. All of these investigations also report considerable variability in female behavior during attendance, but only Kushlan and Kushlan (1979) have attempted any quantification. Although nest defense may have been more common in some parts of the alligator's range than in others (perhaps due to differences in predation patterns), learned avoidance of humans has probably obscured any geographic differences. McIlhenney (1935:86) believed that there had been a considerable decline in nest defense frequency in Louisiana during his lifetime, which he attributed to humans.

The only detailed observations of a female alligator opening a nest are those of E. Meyer (pers. comm.). These indicate that alligators, like other crocodilians in which the behavior has been observed, use their forefeet to dig into the egg cavity from above and, at least in some cases, use their mouths to liberate the young. The similar appearance of all of our opened nests, in conjunction with Meyer's films, suggests that nest-opening behaviors of *A. mississippiensis* are quite stereotyped. This stereotypy may extend to other mound-nesting crocodilians; photographs of opened nests of *Caiman crocodilus* (Staton and Dixon, 1977, Fig. 2) and *Crocodylus porosus* (Webb, 1977, Fig. 20) show the same type of semicircular excavation we have observed in American alligators (Fig. 4).

All species of crocodilians studied have shown elaborate behaviors involving nest site selection, nest construction and maintenance (especially mound nesters), nest defense, liberation of the young, and a variable degree of post-hatching care (Alvarez del Toro, 1974; Cott, 1971; Staton and Dixon, 1977; Hunt, 1975). The Alligatorinae and Crocodylinae have probably been evolutionarily distinct since the late Cretaceous (Sill, 1968); the similarities in nesting behavior between the two subfamilies, while doubtless affected by habitat (Campbell, 1972), suggest considerable antiquity for these patterns. It is extremely interesting that individual alligators are able to modify an innate behavior such as nest defense so readily without altering other behaviors such as nest maintenance or liberation of young. This ability to learn is clearly valuable to an animal which faces a variety of stresses in its lifetime, and is probably an important factor in the persistence of this order.

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