Nesting Ecology of the American Alligator in Southeastern Louisiana

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Abstract: Nesting ecology of the American alligator (*Alligator mississippiensis*) has been extensively studied in southwestern Louisiana, but little data exist from other parts of the state. Nesting ecology was investigated in an intermediate salinity marsh in southeastern Louisiana during 1987 and 1988. We located and examined 53 nests. Nesting habitat included spoilbanks, bulltongue (*Sagittaria lancifolia*) and wiregrass (*Spartina patens*) marshes. Floating marsh was not used. Mean clutch size was 29.4 ± 1.7 eggs and mean egg mass was 64.1 ± 0.3 g. Nest temperatures were within the optimal range of 31 to 32 C. In 1987, 3 (75%) nests on spoilbanks and 4 (36.6%) nests in bulltongue marsh were successful. Remaining nests were destroyed by raccoons or flooding. Nest predation was not observed in 1988, but all nests were lost to flooding from tropical storm Beryl on 9 August.

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Nesting ecology of the American alligator has been extensively studied in the Chenier Plain marshes of southwestern Louisiana (Joanen 1969, Carboneau 1987, Joanen and McNease 1987a). However, little data exist for alligator populations in the deltaic marshes of southeastern Louisiana despite high densities and abundant habitat (McNease and Joanen 1978). McNease and Joanen (1978) reported the highest alligator densities in Louisiana occur in intermediate salinity marshes (1 alligator/3.2 ha), a community type widespread in southeastern Louisiana (Chabreck and Linscombe 1978). Furthermore, intermediate salinity

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marshes had the highest 10-year average alligator nest density (1 nest/31.5 ha) of all marsh types in Louisiana (McNease et al. 1994). Platt et al. (1990a) and Wolfe et al. (1987) have documented alligator food habits in this region. Rootes et al. (1991) found higher growth rates in alligators from moderately saline habitats and suggested that age-specific fecundity rates of females may be higher in these habitats due to greater resource availability. The purpose of this study was to examine nesting ecology of alligators in an intermediate salinity marsh of southeastern Louisiana and make comparisons with studies conducted in other wetland habitats of Louisiana.

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Methods

This study was conducted on the Manchac Wildlife Management Area (MWMA) located within the Lake Pontchartrain estuarine system in St. John the Baptist Parish, Louisiana. MWMA encompasses 3,369 ha of marshland owned by the Louisiana Department of Wildlife and Fisheries (LDWF). Salinities range from 1.0 to 4.6 ppt and are highest in canals and ditches. Vegetation of MWMA has been classified by Chabreck and Linscombe (1978) as the intermediate salinity marsh type dominated by bulltongue (*Sagittaria lancifolia*) and various grasses (*Echinochloa walteri, Panicum dichotomiflorum,* and *Paspalum vaginatum*), scattered with living trees, snags, and logs. Floating marsh dominated by sprangletop grass (*Leptochloa fasicularis*) surrounds a large ($\geq$100 ha), shallow (<0.5-m) body of water known as the "prairie." Wiregrass (*Spartina patens*), a brackish marsh indicator species (Chabreck 1972), is found in a limited area. Spoilbanks are dominated by woody vegetation such as baldcypress (*Taxodium distichum*) and waxmyrtle (*Myrica cerifera*). Platt (1988) provided a history and complete description of the study site.

This study was conducted from late June to early September in 1987 and 1988. Nests were located during aerial surveys conducted by LDWF, plotted on aerial photographs, and later relocated with a Robinson R-22 helicopter. Nests on spoilbanks were concealed by woody vegetation and undetectable from the air. These nests could only be located by foot search. All major spoilbanks on MWMA were searched. In 1988, all but 2 of the 1987 nest sites were revisited and checked for signs of recent activity.

We visited each nest containing eggs at least twice; once in late June or early July, and again in early September. Accessible nests were visited on a weekly or biweekly basis. Nest dimensions were measured to the nearest 0.01 m, and distance from the nest center to the nearest body of water was recorded. Plant species incorporated into the nest, and other components such as logs or stumps were noted. Nests were checked for presence of other reptile eggs and ants (Formicidae). Nesting habitat was classified as bulltongue marsh, wiregrass marsh, floating marsh, or spoilbank (Platt 1988).

We determined air and nest cavity temperatures at each nest. During initial visits, nests were opened and presence of a clutch was determined. Each egg was removed and numbered to maintain an upright orientation and insure proper repositioning in the nest upon closure. Eggs were weighed on spring scales (±1.0 g) and linear dimensions determined with calipers (±0.01 mm). In 1987 a random sample of eggs were weighed and measured. In 1988, all nests were opened to verify presence of eggs, but clutch size was not determined for 10 of these nests. These nests were left undisturbed to determine what effect disturbance had on hatching success. All remaining nests were opened, clutch size determined, and eggs weighed and measured. Alligator tracks found at nest sites were assumed to have been made by nesting females. Rear-foot track length (RTL) was used to estimate snout-vent length (SVL) of nesting females where SVL = 11.94 + 5.08RTL (Platt et al. 1990b). All nests were inspected for signs of predation and flooding. Tracks and patterns of predation were used to identify nest predators. Presence and behavior of any female alligators in the vicinity of nests was noted during aerial surveys and nest inspections.

In 1987, all nests were revisited in late August and early September to determine nesting success. Unhatched eggs and dead hatchlings were noted. In 1988, immediately following the passage of tropical storm Beryl on 9 August, a survey was conducted to determine the extent of flooding on MWMA from storm surge. We attempted to relocate each nest and inspect the clutch. In late August and early September 1988, spotlight surveys were conducted along the major canals to search for hatchlings.

Analysis of variance (ANOVA), Mann Whitney U Test, G-Test, and linear regression and correlation were used for statistical analysis (Sokal and Rohlf 1981). Mean values are reported as ±1 standard error. Results were considered significant at $P \leq 0.05$ unless stated otherwise.

Results and Discussion

Nesting Habitat

In 1987, 19 alligator nests were located and inspected and in 1988, 45 nests were located and 34 inspected (Table 1). The increased number of nests located on MWMA in 1988 is probably from both the improved abilities of investigators, and more efficient marking procedures rather than an increase in nesting activity. Aerial nest count transect data remained constant during both years at 1 nest/45.3 ha (LDWF unpubl. data), somewhat lower than the 10-year average of 1 nest/31.5 ha reported for intermediate marshes (McNease et al. 1994).

Table 1. Nesting habitat and percentage success of alligator nests on Manchac Wildlife Management Area, St. John the Baptist Parish, Louisiana, in 1987 and 1988.

	N Nests		Nesting success (%)	
Habitat	1987	1988	1987	1988
Spoilbank	5	0	3 (75)	—
Bulltongue marsh	14	32	4 (36.3)	0
Wiregrass	0	2	—	0
Total nests	19	34		

Table 2. Alligator nest and clutch characteristics from Manchac Wildlife Management Area, St. John the Baptist Parish, Louisiana, in 1987 and 1988.

Parameter	*N*	Mean±SE	Range
Distance to water (m)	53	4.8±0.7	1.8–19.0
Nest height (m)			
Bulltongue	46	0.40±0.01	0.2– 1.2
Spoilbank	5	0.40±0.06	0.3– 0.6
Wiregrass	2	0.67±0.10	0.5– 0.8
Nest temperature (°C)	93	32.0±0.20	30.0–34.0
Clutch size	32	29.4±1.70	9–49
Egg mass (g)	484	64.1±0.30	44.1–80.0
Egg length (mm)	484	69.8±0.10	61.5–81.4
Egg width (mm)	484	39.3±0.07	34.7–42.3

In 1987 5 (25%) nests were constructed on spoilbanks and 14 (75%) nests were constructed in bulltongue marsh. No nests were found in floating or wiregrass marsh. In 1988, 32 (94%) nests were constructed in bulltongue marsh and 2 (6.0%) in wiregrass marsh. No nests were found on spoilbanks or in floating marsh (Table 1). Floating marsh provides an extremely unconsolidated and unstable substrate that probably could not sustain the weight of a nest or an adult alligator. Spoilbanks may be used as nest sites more frequently than this study indicates as these nests could not be located from the air and proved extremely difficult to locate on the ground. Other studies (Joanen 1969, Dietz and Hines 1980, Wilkinson 1983) have reported spoilbanks and levees to be greatly used as nesting sites where available.

Nest Description

Spoilbank nests averaged 0.40 ± 0.06 m high (N = 5, range = 0.30 to 0.60) and were constructed primarily of soil and woody material. Marsh nests were constructed of bulltongue and wiregrass. Bulltongue nests had a mean height of 0.40 ± 0.01 m (N = 46, range = 0.20 to 1.20) and wiregrass nests had a mean height of 0.67 ± 0.12 (N = 2, range = 0.55 to 0.80) (Table 2). Nest size is dependent on available nesting materials (Metzen 1977), and plant materials incorporated into the nest reflect their availability at the nest site (Joanen 1969, Webb et al. 1977, Goodwin and Marion 1978, Carboneau 1987). Elevated incubation temperatures leading to high levels of egg mortality have been reported in bulltongue nests (Elsey et al. 1994) but was not observed on MWMA. Logs, stumps, and other debris were incorporated into 21 (39.6%) nests. The widespread use of woody debris in alligator nests has not been previously reported and is probably a reflection of its abundance on MWMA.

Nests averaged 4.8 ± 0.7 m (N = 53, range = 1.8 to 19.0) from the nearest body of water (Table 2). Factors influencing positioning of the nest relative to water are not well understood and may depend on the female's position in the breeding hierarchy (Vliet 1987) with high-ranking females obtaining nest sites close to water and lower-ranking females forced into suboptimal habitat farther away. Ideally, nests should be located sufficiently close to water to allow the female to remain in attendance and guard against predators, but far enough away to avoid flooding.

Spot nest temperatures averaged 32.0 ± 0.2 C (N = 93, range = 30.0 to 34.0) (Table 2) and air temperatures averaged 31.1 ± 0.2 C (N = 93, range = 29.0 to 34.0). Nest temperatures were significantly greater than air temperatures (Mann Whitney u-Test; z = 2.684; P = 0.007) and similar to those reported in previous studies (Joanen 1969, Chabreck 1973, Dietz and Hines 1980, Wilkinson 1983, Schulte 1989). Because daily fluctuations are minimal, spot temperatures provide a good approximation of the incubation environment (Chabreck 1973, Magnusson and Taylor 1980, Schulte 1989). Nest temperatures at MWMA were within the optimal range of 31 to 32 C, the common mean incubation temperature reported in most field studies of mound nesting crocodilians (Webb et al. 1987).

Two of 15 active nests (13.0%) in 1987 and 3 of 28 active nests (10.7%) in 1988 contained ant nests. Mortality of eggs or hatchlings attributable to ants was not observed. No other commensal nest fauna or reptile eggs were noted. Ant colonies have been reported in alligator nests in other Louisiana studies (Joanen 1969, Carboneau 1987) and may act as cleaning agents to rid nests of fungal growth and rotted eggs that emit odors which could attract predators (Staton and Dixon 1977). Additionally, complex temperature and humidity relationships are maintained within ant colonies (Holldobler and Wilson 1990), which may influence alligator nest temperatures.

Clutch Characteristics

In 1987, 15 of 19 (80%) nests were active and contained eggs but 4 (26%) of these clutches were lost to predators before clutch size could be determined. Mean clutch size in 1987 was 29.3 ± 3.3 (N = 11, range = 14 to 49). In 1988, 28 of 34 (82.0%) nests were active and 23 nests were opened and clutch size determined. Two of these nests contained partial clutches of decomposing eggs and were not included in clutch size analysis. Mean clutch size in 1988 was 29.8 ± 2.1 (N = 21, range = 9 to 45). There was no significant difference between

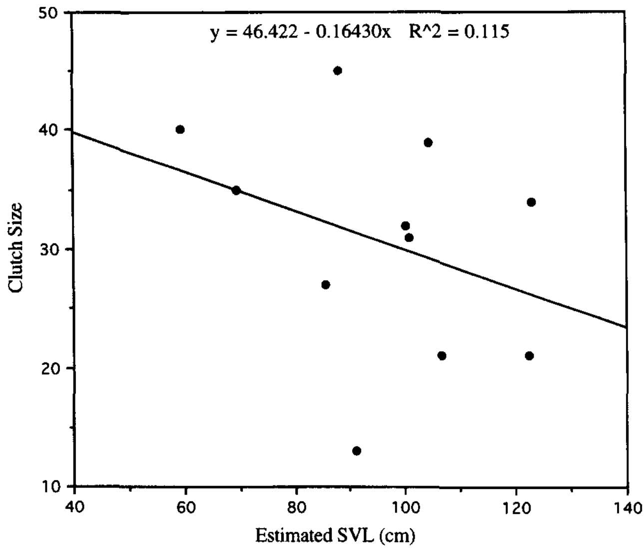

Figure 1. Relationship between estimated snout-vent length (SVL) of nesting female alligators and clutch size on Manchac Wildlife Management Area, Louisiana. SVL estimated from measurements of rear foot track length (RTL) made at nests, where SVL = 11.94 + 5.08RTL (Platt et al. 1990b).

clutch size in 1987 and 1988 (ANOVA; df = 1,29; $F = 0.021$). Mean clutch size for both years was 29.4 ± 1.7 (Table 2). Mean egg mass in 1987 was 62.2 ± 1.5 g ($N = 30$, range = 44.1 to 76.0) and in 1988 was 64.5 ± 0.31 g ($N = 454$, range = 48.0 to 80.0). Mean egg mass in 1987 and 1988 did not significantly differ (ANOVA, df = 1,484; $F = 0.07$). Mean egg mass for both years was 64.1 ± 0.3 g (Table 2). Mean egg length was 69.8 ± 0.1 mm ($N = 484$, range = 61.5 to 81.4) and mean egg width was 39.3 ± 0.07 mm ($N = 484$, range = 34.7 to 42.3) (Table 2).

Tracks of measurable quality were found at 11 nests and used to estimate female SVL. Estimated female SVL was not significantly correlated with clutch size ($r = -0.33$, df = 9) on MWMA, possibly due to our small sample size (Figure 1). Ferguson (1985) stated there is a significant positive, but highly variable correlation between clutch size and female length. Variability may mask this relationship unless sample size is large.

Mean clutch size on MWMA was lower than the mean clutch size of 38.9 (range = 2 to 58) reported for Rockefeller Refuge (Joanen 1969) but not significantly different from the mean clutch size of 33.2 ± 3.04 ($N = 41$) reported by Carboneau (1987) for Lacassine NWR (ANOVA; $F = 1.06$, df = 1,71). The reasons for these differences are unclear, but may be attributed to size and age distributions, nutritional status, or geographic variation (Ferguson 1985, Joanen and McNease 1987, Rootes et al. 1991).

Four of 19 (21.0%) and six of 34 (17%) nests were inactive in 1987 and 1988, respectively, and contained no eggs. These were fully formed nests, indistinguishable from active nests. False nesting occurs among most mound nesting crocodilians (Joanen 1969, Webb et al. 1977, Goodwin and Marion 1978, Metzen 1977, Dietz and Hines 1980, Wilkinson 1983). Four nests on MWMA were within 10 m of an active nest and it was assumed they were constructed by the same female. However, the remainder of false nests were isolated, and it is not known if females moved to other sites or simply failed to produce clutches and then abandoned the nests. False nesting is poorly understood and has been attributed to abandonment following disturbance by humans or predators or nesting efforts of reproductively immature females (Webb et al. 1977).

Nesting Success

Two clutches in 1987 and 1988 (13.0% and 7.1%, respectively) were lost to flooding during periods of elevated water levels in late June and July (Table 1). Three clutches (20.0%) in 1987 and 2 clutches (7.1%) in 1988 also lost a small number of eggs from partial innundation of the nest. All nests subject to flooding were located in bulltongue marsh. Six clutches (13.9%) were destroyed by predators in 1987. These included one spoilbank nest (6.6%) and 5 marsh nests (3.3%). No nests were lost to predators in 1988.

Nesting success was 46.6% in 1987. Three spoilbank nests (75.0%) and 4 marsh nests (36.3%) were successful (i.e., produced at least one viable hatchling). Nesting success of spoilbank nests was significantly greater than marsh nests (G-test, df = 1, $G = 8.198$). The earliest hatching occurred on 19 August. Hatching of all nests was completed by 12 September. All successful nests were opened by attending females with 1 exception. This nest was opened by investigators on 19 September and contained 13 recently hatched eggs and 34 unhatched eggs. The hatchlings liberated themselves from the nest.

There were no successful nests in 1988. On 9 August, tropical storm Beryl made landfall on the Louisiana Gulf Coast and the resulting floodwaters completely innundated all marked nests. Water levels were approximately 15.0 cm above the top of the nests on 10 August and eggs remained submerged for 72 to 96 hours, resulting in total clutch mortality in 24 nests examined. Four previously marked nests could not be relocated following passage of the storm. Submergence for 12 or more hours will result in embryonic death by inhibiting oxygen diffusion through the eggshell (Joanen et al. 1977, Ferguson 1985). No hatchlings were observed during night surveys conducted in early September and it is believed that no alligator nests on MWMA were successful in 1988.

All clutch mortality observed in this study was from flooding and predation, both significant factors in nest failure (Joanen 1969, Fleming et al. 1976, Metzen 1977, Goodwin and Marion 1978, Dietz and Hines 1980, Wilkinson 1983, Hunt and Ogden 1991, Kushlan and Jacobsen 1990). Flooding early in the nesting season during both years of this study was from increased water levels from southeasterly winds forcing water into the marsh from Lake Pontchartrain.

Raccoons (*Procyon lotor*) are the major nest predator in Louisiana (Joanen 1969, Fleming et al. 1976) and all cases of nest predation on MWMA were attributed to raccoons. Patterns of predation match those described by Joanen

(1969) and Dietz and Hines (1980). Raccoons opened nests through a single entry hole and then consumed all or part of the clutch. Uneaten eggs and eggshells were often scattered about the nest site.

It is not known why predation rates were so much greater in 1987 than 1988. Joanen (1969) found that predation by raccoons is most likely to occur after the seventh week of incubation and hatchling vocalizations from within the nest often attract predators late in incubation (S. Platt pers. observ.). Tropical storm Beryl may have preempted predation that would have otherwise occurred later. Nest predation appears dependent on environmental factors which influence availability of other raccoon foods (Fleming et al. 1976).

The higher nesting success among spoilbank nests on MWMA was attributed to the elevated substrate preventing submergence during high water periods, and proximity of permanent water in adjacent canals allowing females to remain in attendance and defend nests from raccoons throughout incubation. Marsh nests were subject to higher predation during drought when potholes adjacent to nests dried out and females were forced to seek deeper pools, leaving nests unguarded. Hunt and Ogden (1991) found predation to be significantly associated with water levels, with higher predation during low water periods.

Hurricanes and tropical storms may substantially reduce nesting success among alligator populations along the Louisiana Gulf Coast more frequently than previous studies indicate. Fleming et al. (1976) reported nest losses of 53% from tropical storm Delia in 1973. Our study is the first to document total nest loss from a tropical storm. Tropical disturbances occur along the Louisiana Gulf Coast with expected frequencies ranging from 38 per 100 years in southwestern Louisiana, 63 per 100 years in the Mississippi delta, and 45 per 100 years in southeastern Louisiana (Newton 1986). Highest frequencies occur in July, August, and September (Newton 1986), coinciding with the alligator nesting season (Lance 1989). Tropical storm Beryl was a comparatively minor event with winds not exceeding 50 mph and effecting a relatively localized region (National Weather Service, Baton Rouge, unpubl. Data). A major hurricane would likely result in total nest loss throughout much of Louisiana's coastal zone.

Female Behavior

Although nest site fidelity has been reported for the American alligator (McIlhenny 1935, Lance 1989) only one instance of nest site reuse on MWMA was found in 1988. Joanen (1969) and Carboneau (1987) found 1.3% and 4.1%, respectively, of alligator nests were located at a previous year's nest site. It remains unclear if nest sites are being reused by the same or different female alligators. Individual females do not nest annually (Lance 1989, Wilkinson 1983), and it is likely that longer term studies may be necessary to detect patterns of nest site reuse.

Active nest defense was observed only once when a female made aggressive movements towards a hovering helicopter. Females were observed at nests during aerial surveys and routine visits, and tracks and dens were found at nest sites. It is believed females were probably avoiding humans, but defending nests against predators. Nesting females will respond differently to various nest predators (Hunt and Ogden 1991) and aggressive behavior toward human investigators may not be an accurate index of actual nest defense (Wilkinson 1983).

The low incidence of nest defense behavior toward humans on MWMA also may result from hunting pressure. Previous studies suggest that hunting pressure may modify behavioral responses toward humans. McIlhenny (1935) stated that only where alligators are not hunted will they defend nests; Joanen and McNease (1971) found that following traumatic encounters with humans, female alligators may cease nest defense behavior; and Wilkinson (1983) observed that nest defense behavior was confined to areas where alligators have experienced long-term protection. Furthermore, nest defense behavior was not recorded on Lacassine NWR (Carboneau 1987) where an annual harvest is conducted, while on Rockefeller Refuge, which is closed to hunting, 9.2% of female alligators defended nests against humans (Joanen 1969).

In summary, nesting alligators in southeastern Louisiana used stable marsh substrates or spoilbanks for nest construction. Nest temperatures were within the optimal range of most mound nesting crocodilians. Clutch sizes differed from other studies in Louisiana, possibly due to size and age distributions, nutritional status, or geographic variation. Passage of tropical storm Beryl in 1988 resulted in complete nest loss.

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