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Nesting Ecology of the American Crocodile in the Coastal Zone of Belize

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We conducted a study of American Crocodile nesting ecology in coastal Belize from June 1996 to July 1997. Most nesting areas were found on elevated beach ridges composed of coarse sand. Shallow, brackish lagoons adjacent to nesting areas provide critical nursery habitat for hatchlings. The most significant nesting areas were found in the Turneffe Atoll. American crocodiles construct both hole and mound nests in Belize. Clutches are deposited during the last half of the dry season, from late March to early May. Mean clutch size is 22.3 ± 6.0 eggs. Hatching occurred from late June to mid-July, a period coinciding with the beginning of the wet season. Nesting success was high, and losses to predation and flooding were negligible. Females may defend nests from predators and excavate neonates at hatching, but otherwise parental care appears minimal. The protection of suitable nesting and nursery habitat is essential for the continued survival of the American crocodile in Belize.

THE American Crocodile (*Crocodylus acutus*) is widely distributed in the northern Neotropics on the Atlantic and Pacific coasts of Mexico, Central America, and northern South America, many Caribbean islands, and the southern tip of Florida (Thorbjarnarson, 1989). Populations have declined throughout much of this range because of past overexploitation, continued illegal hunting, and habitat destruction. The American crocodile is currently considered vulnerable by the International Union for the Conservation of Nature and Natural Resources (IUCN) and listed on Appendix I of the Convention on Trade in Endangered Species of Flora and Fauna (Thorbjarnarson, 1992; Ross, 1998). One of the largest remaining regional populations is believed to occur in Belize (Ross, 1998), where *C. acutus* is extremely rare on the mainland and largely confined to offshore cays (islands) and atolls (unpubl. data). This population was seriously depleted by overharvesting in the past, and there is little evidence of recovery. The American crocodile is considered threatened by the Coastal Zone Management Program, Government of Belize (McField et al., 1996). Despite its threatened status, the reproductive ecology of the American crocodile in Belize remains poorly known. Such information is an essential element in planning effective conservation strategies for endangered crocodilians (Thorbjarnarson and Hernandez, 1993).

MATERIALS AND METHODS

Fieldwork was conducted from July 1996 to September 1997 throughout the coastal zone in conjunction with a countrywide survey of *C. acutus* in Belize. The coastal zone encompasses all offshore cays and atolls and all wetlands, both freshwater and saline, within 10 km of the Caribbean Sea (McField et al., 1996). Place names correspond to topographic maps issued by the Ordnance Survey, Southampton, England.

Potential habitat was located by boat and searched on foot to find nesting areas, which were identified by the presence of excavated nests, eggshells, and eggshell membranes. These sites were revisited in April and May 1997. Nests were located by noting fresh tracks and disturbances in the sand and carefully excavated to expose the clutch. The distance from the soil surface to the top of the clutch was measured, and all eggs were removed and counted. Eggs were numbered on the dorsal surface to ensure proper positioning and orientation when replaced. All eggs were weighed with a Pesola spring scale (± 0.5 g), and length and width were measured with dial calipers (± 0.1 mm). Egg viability was determined by the presence of opaque bands, and date of oviposition was estimated based on the extent of banding (Ferguson, 1985). The diameter and depth of the egg chamber and distance to water were measured after the clutch was removed. The total length (TL) of nesting females was estimated from the length of rear-foot tracks found at nests (Platt et al., 1990). Based on measurements of 48 *C. acutus* captured during a concurrent population study (unpubl. data), rear-foot length (RFL) was found to be a good predictor of total length ($TL = 11.64RFL + 4.9$; $r^2 = 0.87$; $P < 0.001$).

Return visits were made to most nests to determine nesting success, defined as those nests

from which at least one egg hatched. Neonates were captured within two weeks of hatching, measured [total length; snout–vent length (SVL)] to the nearest 0.1 cm, weighed to the nearest 0.5 g, marked and released at the site of capture. Mean values are presented as ± 1 SD. Results are considered significant at $P \leq 0.05$.

Results and Discussion

Twelve nesting areas were identified in the coastal zone of Belize. The number of nests at each area ranged from one to 10. The most significant nesting areas were located on Blackbird (17°19′N, 87°47′W) and Northern (17°29′N, 87°47′W) Cays in the Turneffe Atoll, where up to 15 clutches may be deposited annually (unpubl. data). Eight nesting areas (66.7%) were found on elevated beach ridges, three (25.0%) on spoilbanks, and one (8.3%) on a low-relief beach. Elevated beach ridges composed of coarse sand seem to be the preferred nesting habitat in Belize. These sparsely vegetated beaches are usually found on the eastern (windward) shoreline of cays where exposure to wave-action and elevation are greatest. Elevated beaches minimize the chance of nest flooding, and the coarse substrate allows ample oxygen diffusion to the eggs (Mazzotti et al., 1986).

Nesting occurred in multiple years at 10 of 11 areas (91.0%) for which more than one year of data was available. Evidence of colonial nesting (more than one nest) was found at five (41.6%) areas. The reuse of nesting areas and colonial nesting among *C. acutus* is common and believed to occur when suitable nesting habitat is limited (Thorbjarnarson, 1989).

Shallow, brackish lagoons were adjacent to four (33%) nesting areas and provide critical nursery habitat and a source of drinking water for hatchlings. Hatchlings cannot maintain body mass in seawater (36 ppt; Dunson, 1982), so access to fresh or brackish (≤ 10 ppt) water is necessary for osmoregulation (Mazzotti et al., 1986). Survival is typically high where nursery habitat is available (Kushlan and Mazzotti, 1989). At nesting areas in Belize lacking nursery habitat, hatchlings may be subject to prolonged periods of osmotic stress resulting in decreased growth and survival.

Crocodile tracks, drag marks, and shallow, exploratory holes were found at nesting areas during late March and early April 1997. Thirteen clutches were found from 4 April to 25 June 1997, and estimated date of oviposition ranged from 29 March to 5 May 1997 with a mean date of 14 April ± 10.8 days. This period coincides with the last half of the dry season and is similar to nesting periods elsewhere in the Caribbean (Thorbjarnarson, 1989). Although mating behavior was not observed, courtship activity typically begins one to two months prior to nesting (Thorbjarnarson, 1989). Thus, in Belize, courtship and mating probably commence in February and peak in March, a period during which groups of up to 10 adult crocodiles were observed in shallow water off nesting beaches in the Turneffe Atoll.

Table 1. Characteristics of Hole Nests and Clutch Attributes of the American Crocodile in Belize (1996 to 1997).

Parameter	Mean ± 1 SD	Range	n
Nest characteristics			
Depth to top of clutch (cm)	23.3 ± 6.3	17–32	11
Depth to bottom of clutch (cm)	32.8 ± 5.4	22–40	11
Width of hole (cm)	26.0 ± 8.6	20–35	11
Distance to water (m)	8.5 ± 4.1	3.0–16.7	11
Clutch attributes			
Clutch size	22.3 ± 6.0	12–32	14
Egg length (mm)	70.5 ± 4.3	60.6–88.3	304
Egg width (mm)	44.1 ± 1.6	39.2–50.0	304
Egg mass (g)	85.6 ± 9.7	61.5–111.0	280
Clutch mass (kg)	1.8 ± 0.8	0.9–3.1	13
Nonviable eggs (%)	46.5 ± 41.7	0.0–86.6	10

Twelve active nests containing 14 clutches were found during this study: eight in the Turneffe Atoll, and one each from Belize City (17°30′N, 88°12′W), Cay Caulker (17°44′N, 88°01′W), Maps Cay (17°29′N, 88°05′W), and Southern Lagoon (17°15′N, 88°20′W), respectively. These included one mound and 11 hole nests. The mound nest was constructed on a low beach, slightly elevated above normal high tide level and about 3 m from an old mound nest located during a preliminary survey in 1994 (Platt and Thorbjarnarson, 1996). Both mounds were well-defined piles of sand and leaf litter, measuring approximately 200 × 160 cm wide and 30 cm high. Similar mound nests have been reported only among American crocodile populations in Florida (Ogden, 1978; Kushlan and Mazzotti, 1989) and may be an adaptive response to nesting in low-lying areas where the probability of flooding is high (Campbell, 1972; Thorbjarnarson, 1989). The remaining were hole nests, although some were slightly mounded (< 10 cm). The mean dimensions of 11 hole nests are presented in Table 1.

Two nests contained double clutches representing the reproductive efforts of multiple fe-

males. Different clutches were readily distinguished by a notable discrepancy in egg size and the extent of opaque banding. Two clutches in one mound nest were deposited adjacent to each other, and the majority of eggs in both appeared viable and hatched successfully. A clutch deposited in a hole nest was unearthed by a second female, who then laid another clutch in the hole. The eggs from the first clutch were scattered about the surface and no longer viable.

Of the 14 clutches examined during this study, one was found in 1996 and 13 in 1997. Clutch attributes are summarized in Table 1. There was no correlation between clutch size and Julian date of oviposition ($r = -0.14$; $P = 0.65$; n = 13). Mean clutch size differed between populations in Belize, Haiti (22.5 ± 2.7; n = 14; Thorbjarnarson, 1988), and Florida (38.0 ± 9.4; n = 46; Kushlan and Mazzotti, 1989; and 45.2 ± 17.2; n = 20; Ogden, 1978; ANOVA; $F_{2,71} = 18.95$; $P < 0.001$). Mean clutch size was significantly less in Belize and Haiti than in Florida (Tukey-Kramer MSD). Mean egg mass did not differ significantly between Belize and Haiti (97.0 ± 8.1 g; n = 68; Thorbjarnarson, 1988; ANOVA; $F_{1,346} = 0.56$), although mean clutch mass in Haiti (2.18 kg; Thorbjarnarson, 1988) was somewhat larger. Unfortunately, neither egg or clutch mass have been widely reported by previous workers.

The small clutch size, egg mass, and clutch mass found among *C. acutus* in Belize may be a result of the small body size of reproducing females. The relationship of clutch size, egg mass, and clutch mass with female body size is highly variable among crocodilians, but in general these parameters increase with increasing female body size (Thorbjarnarson, 1996). The size of female *C. acutus* at first reproduction ranges from 2.1–3.0 m (Thorbjarnarson, 1989), but in Belize much smaller females may be capable of reproducing. A blood sample collected in February 1997 from a 1.8-m female contained a large amount of visible fat, suggesting vitellogenesis was occurring. Additionally, the TL of two females estimated from the length of rear-foot tracks found at nests was 1.9 and 2.0 m. We also noted a trend toward small adult body size among males, although whether this was becasuse of genetic and environmental factors or past overharvesting remains unknown (unpubl. data). Reproductive output may be further constrained by resource availability, nutritional limitations, and the high metabolic costs associated with inhabiting a marine environment.

Levels of egg viability could not be determined for four clutches: one contained rotten eggs, and bands could not be distinguished; and three were found within 12 h of oviposition before bands became evident (usually 24 h after laying; Ferguson, 1985). The remaining 10 clutches contained 225 eggs of which 43 were nonviable (19.1%). However, 26 nonviable eggs were from a single nest at the municipal dump on Cay Caulker. If this clutch is removed from the analysis, then an adjusted value of 8.7% is calculated, similar to the 10% and 9.9% levels of nonviability reported from Florida (Kushlan and Mazzotti, 1989) and Haiti (Thorbjarnarson, 1988), respectively.

Hatching dates were determined for two nests with known oviposition dates on Northern Cay, Turneffe Atoll, and incubation periods were 78 and 81 days. Other clutches hatched from late June to mid-July, although the precise hatching dates were unknown. Hatchling emergence in Belize coincides with the beginning of the wet season, and June is the month of greatest rainfall (Johnson, 1983). Hatchlings cannot maintain body mass under saline conditions (Dunson, 1982) and depend on rainfall events for rehydration (Mazzotti et al., 1986). Thus, the seasonal distribution of rainfall is as important as the amount of rain and exerts a strong influence over hatchling growth rates and survival (Moler and Abercrombie, 1992).

Nesting success appears to be high among *C. acutus* in Belize, since eight (80.0%) of the 10 clutches of which the fate was known were successful. Successful nests were recognized by the presence of pipped eggshell membranes, and signs indicating the nest was excavated by an adult, presumably the nesting female. Two clutches failed to hatch; one apparently desiccated, and another was composed almost entirely of nonviable eggs. The fate of four clutches could not be determined.

Nest failure among *C. acutus* populations elsewhere is generally attributed to flooding or nest predation, with minor losses from other causes such as unsuitable thermal regimes or desiccation (Thorbjarnarson, 1989). Flooding does not appear to be a major source of failure in Belize, because most nests are constructed on substrates not subject to inundation. Raccoons (*Procyon lotor*) are a major nest predator elsewhere (Kushlan and Mazzotti, 1989) and occur throughout the Turneffe Atoll and on many cays. Although we previously documented the destruction of one nest by raccoons (Platt and Thorbjarnarson, 1996), no further losses were noted and predation appears rare. Alternate food resources such as crabs are abundant, and Fleming et al. (1976) concluded raccoon pre-

dation of American Alligator (*Alligator mississippiensis*) nests was dependent on the availability of alternate foods, with predation being lowest when crawfish were most abundant.

Nest defense behavior by female *C. acutus* is highly variable; females in some areas actively defend nests, whereas elsewhere little or no nest protection is provided (Thorbjarnarson, 1989). We did not encounter nest defense behavior directed toward investigators but found fresh tracks at nest sites and observed large adults nearby during incubation, suggesting females may protect nests from predators. Although aggressive behavior toward human investigators is used as an index of nest defense in many studies, females may defend nests against small mammalian predators but selectively avoid humans (P. M. Wilkinson, South Carolina Wildlife and Marine Resources Dept., 1983, unpubl.).

Twenty one-week-old (identified by an open umbilical scar) hatchlings were captured in July 1997 at a nursery lagoon on Northern Cay, Turneffe Atoll. Morphometric attributes are as follows: SVL = 13.2 ± 0.5 cm (range = 12.4–14.5 cm); TL = 27.9 ± 1.2 cm (range = 26.2–31.0 cm); mass = 58.5 ± 0.4 g (range = 46.0–67.0 g). Maternal care of neonates appears minimal among *C. acutus* in Belize. Females excavated all successful nests and, based on an interpretation of sign, transported neonates to water. Adults were present in the nursery lagoon on Northern Cay, Turneffe Atoll, shortly after hatchling emergence in August 1996 and June–July 1997 and responded to hatchling distress calls during capture. However, during population surveys (unpubl. data), solitary hatchlings and small juveniles were encountered at widely separated locations, suggesting true pod formation occurs only briefly after hatching or not at all among *C. acutus* in Belize. Other studies also indicate an extended period of maternal care is lacking in the American crocodile (Rodda, 1984; Thorbjarnarson, 1988; Kushlan and Mazzotti, 1989).

The timing of hatchling dispersal was variable. No hatchlings were found at the nursery lagoon on Northern Cay, Turneffe Atoll, in late August 1997, whereas in a similar lagoon on Long Cay (17°37′N, 88°03′W), juveniles that probably hatched in 1996 (based on TL) were still present in February 1997. On Northern Cay, the large number of hatchlings (at least 200 from 10 nests) may have rapidly depleted available food resources thereby prompting an early dispersal, whereas on Long Cay (two nests in 1996), hatchling numbers may have been insufficient to deplete resources, and hatchlings remained near the natal beach. A similar resource depletion model has been proposed to explain home range dispersion patterns of *C. acutus* (Rodda, 1984) and daily movement away from a communal retreat by hatchling American alligators (Dietz and Hines, 1980). Hatchlings were never found near sites lacking nursery habitat, and dispersal from these sites probably occurred immediately after hatching (Kushlan and Mazzotti, 1989).

In conclusion, successful nesting of *C. acutus* in Belize is dependent on a combination of elevated beach ridges and nearby brackish lagoons to serve as nursery habitat. Such habitat is rare because of natural and anthropogenic factors. Most cays lack beach ridges, and other beaches are under increasing pressure for development because they are often the only elevated ground in an area otherwise only slightly above sea level. Indeed, residential and tourist development on Ambergris Cay (17°53′N, 87°58′W) has destroyed the largest continuous beach in Belize, which was formerly important crocodile and marine turtle nesting habitat (McField et al., 1996; unpubl. data). Without protection of suitable nesting and nursery habitat, the long-term survival of *C. acutus* in Belize is doubtful.

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Literature Cited

Campbell, H. W. 1972. Ecological or phylogenetic interpretations of crocodilian nesting habits. Nature 238:404–405.

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

Dunson, W. A. 1982. Salinity relations of crocodiles in Florida Bay. *Ibid.* 1982:374–385.

Ferguson, M. W. J. 1985. Reproductive biology and embryology of the crocodilians, p. 329–491. *In:* Bi-

ology of the Reptilia. Vol. 14. Development A. C. Gans, F. Billet, and P. F. A. Maderson (eds.). John Wiley and Sons, New York.

FLEMING, D. M., A. W. PALMISANO, AND T. JOANEN. 1976. Food habits of coastal marsh raccoons with observations of alligator nest predation. Proc. Ann. Conf. Southeast. Assoc. Game Fish Comm. 30:348–357.

JOHNSON, W. C. 1983. The physical setting: northern Belize and Pulltrouser Swamp, p. 8–20. *In:* Pulltrouser Swamp: ancient Maya habitat, agriculture, and settlement in northern Belize. B. L. Turner and P. D. Harrison (eds.). Univ. of Texas Press, Austin.

KUSHLAN, J. A., AND F. J. MAZZOTTI. 1989. Population biology of the American crocodile. J. Herpetol. 23: 7–21.

MAZZOTTI, F. J., B. BOHNSACK, M. P. MCMAHON, AND J. R. WILCOX. 1986. Field and laboratory observations on the effects of high temperature and salinity on hatchling *Crocodylus acutus*. Herpetologica 42: 191–196.

MCFIELD, M., S. WELLS, AND J. GIBSON. 1996. State of the Coastal Zone report, Belize, 1995. Coastal Zone Management Programme, and United Nations Development Programme and Global Environmental Facility. Government Printing Office, Belmopan, Belize.

MOLER, P., AND C. L. ABERCROMBIE. 1992. Growth and survival of *Crocodylus acutus* in South Florida, USA, p. 272–289. *In:* Crocodiles. Proceedings of 11th working meeting of crocodile specialist group, IUCN, Gland, Switzerland.

OGDEN, J. C. 1978. Status and nesting biology of the American crocodile, *Crocodylus acutus*, (Reptilia, Crocodilidae) in Florida. J. Herpetol. 12:183–196.

PLATT, S. G., AND J. B. THORBJARNARSON. 1996. Preliminary assessment of the status of the American crocodile (*Crocodylus acutus*) in the coastal zone of Belize, p. 184–206. *In:* Crocodiles. Proceedings 13th working meeting of crocodile specialist group, IUCN, Gland, Switzerland.

———, C. G. BRANTLEY, R. S. CROPANZANO, AND R. W. HASTINGS. 1990. A method for estimating the size of nesting female alligators. Wildl. Soc. Bull. 18: 296–298.

RODDA, G. H. 1984. Movements of juvenile American crocodiles in Gatun Lake, Panama. Herpetologica 40:444–451.

ROSS, J. P. 1998. Crocodiles: Status survey and conservation action plan. 2nd ed. IUCN/SSC Croc. Spec. Group, Gland, Switzerland.

THORBJARNARSON, J. B. 1988. The status and ecology of the American crocodile in Haiti. Bull. Florida St. Mus., Biol. Sci. 33:1–86.

———. 1989. Ecology of the American crocodile (*Crocodylus acutus*), p. 228–258. *In:* Crocodiles: their ecology, management, and conservation. IUCN-The World Conservation Union Publ., Gland, Switzerland.

——— (COMP.). 1992. Crocodiles: an action plan for their conservation. H. Messel, F. W. King, and J. P. Ross (eds.). IUCN/SSC Croc. Spec. Group Publ., Gland, Switzerland.

———. 1996. Reproductive characteristics of the order Crocodylia. Herpetologica 52:8–24.

———, AND G. HERNANDEZ. 1993. Recent investigations of the status and distribution of the Orinoco crocodile *Crocodylus intermedius* in Venezuela. Biol. Conserv. 62:179–188.

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