

Reproductive dynamics of a tropical freshwater crocodylian: Morelet's crocodile in northern Belize

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Abstract

Morelet's crocodile *Crocodylus moreletii* has not been well-studied and many aspects of its life history are unknown. In particular there is a notable paucity of information on nesting and reproductive ecology. We studied the nesting ecology of Morelet's crocodile in northern Belize from 1992 through 1995. Nesting occurs at the onset of the wet season in mid-June and continues through mid-July (mean oviposition date = 1 July \pm 10 days). Eggs hatch from mid-August through mid-to late September. Nesting effort at our primary study site remained relatively constant during 1992, 1993 and 1995, but nearly doubled in 1994; this appeared to reflect a regional trend. Natural and man-made islands are heavily used as nesting sites. Nesting success in 1993 and 1994 was consistently higher on natural islands when compared with man-made islands or shoreline sites. Nest losses were primarily due to flooding and raccoon *Procyon lotor* predation. Losses from predation were greatest in 1994 when unseasonably low water levels facilitated predator access to nests. Females probably reach sexual maturity in 7–8 years after attaining a total length of 150 cm. Mean clutch size (25.0 ± 7.6 ; range = 9–42; $n = 73$) did not differ among years. Mean clutch size, egg width (EW), egg length, egg mass (EM) and clutch mass were positively correlated with female snout–vent length (SVL). Mean EW was the best predictor of female SVL. A partial correlation analysis of egg and clutch attributes found that independent of female SVL, EM increases with increasing clutch size.

Introduction

Morelet's crocodile *Crocodylus moreletii* is a large crocodylian (total length [TL] to 416 cm; Perez-Higareda, Rangel-Rangel & Smith, 1991) inhabiting freshwater wetlands throughout much of the Atlantic lowlands of Mexico, Guatemala and Belize (Groombridge, 1987). Early writers frequently commented on the abundance of *C. moreletii* in Belize (formerly British Honduras) (Schmidt, 1924; Sanderson, 1941; Neill & Allen, 1959), but over-harvesting for its commercially valuable skin in the years following World War II resulted in widespread regional population declines (Powell, 1972; Alvarez del Toro, 1974). By the mid-1970s Morelet's crocodile was nearly extirpated from Belize with the few remaining populations confined to remote regions of the country (Frost, 1974; Abercrombie *et al.*, 1980). Morelet's crocodile was recognized as Endangered by the United States Endangered Species Act, listed on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora, and afforded complete legal

protection in Belize under the Wildlife Protection Act of 1981 (Platt & Thorbjarnarson, 2000a). Populations responded vigorously to legal protection, and surveys during the 1990s found *C. moreletii* to be widespread and abundant in Belize, even within human modified landscapes (Rainwater, Platt & McMurry, 1998; Platt & Thorbjarnarson, 2000a). More recent observations indicate that most suitable wetland habitat in northern Belize is now occupied by *C. moreletii* (S. G. Platt *et al.*, unpubl. data). Indeed, populations have increased to such an extent that complaints to the Belize Forest Department concerning nuisance crocodiles in urban areas are now commonplace (Windsor *et al.*, 2002; Garel, Rainwater & Platt, 2005). Morelet's crocodile is currently listed by the International Union for the Conservation of Nature and Natural Resources (IUCN, 2004) as a species with a low risk of extinction, but 'conservation dependent' meaning that continued survival is contingent on the success of current conservation programs (Ross, 1996).

Despite conservation concerns, *C. moreletii* has not been well-studied and many aspects of its life history remain

largely unknown (Platt, 1996). In particular there is a notable paucity of information on the nesting and reproductive ecology of *C. moreletii*, the only fully mound nesting species of *Crocodylus* in the New World (Thorbjarnarson, 1992). Alvarez del Toro (1974) provides a largely anecdotal account with some discussion of nesting, Hunt (1973, 1975, 1977) reported on maternal behavior and captive propagation, and others present fragmentary data on various aspects of reproduction (Campbell, 1972a; Brazaitis, 1973; Perez-Higareda, 1980; Casas-Andreu & Rogel-Bahena, 1986; Sigler & Gonzalez Blanco, 1994; Sigler & Marina, 2004); however, detailed field investigations into the nesting ecology of *C. moreletii* are lacking. Such studies are essential in planning effective conservation strategies for poorly known species of crocodylians (Thorbjarnarson & Hernandez, 1993). Moreover, while crocodylians exhibit a suite of life history characteristics unique among vertebrates (e.g. large body size, long reproductive lifespan, the production of large numbers of relatively small offspring and complex parental care behavior), life history analyses have been hampered by a lack of quantitative field studies (Thorbjarnarson, 1994). We present here the results of a 4-year study of Morelet's crocodile nesting ecology in wetlands of northern Belize. In this study we describe nests and nesting phenology, characterize nesting habitat, determine nesting success and quantify allometric relationships between reproductive females, clutch size and egg attributes.

Study area

We studied the nesting ecology of *C. moreletii* in wetlands throughout northern Belize (Belize, Cayo, Corozal and Orange Walk Districts), a region characterized by alluvial floodplains and interfluvial swampy depressions and sinkholes (Alcala-Herrera *et al.*, 1994). Natural wetlands occupy up to 40% of the lowlands in northern Belize (Alcala-Herrera *et al.*, 1994) and generally contain water throughout the year, although levels fluctuate and periodic episodes of drought may occur (Darch, 1983). Freshwater wetlands are often heavily vegetated with *Cladium jamaicense*, *Typha domingensis*, *Eleocharis* spp. and *Nymphaea* spp., while coastal wetlands are typified by moderately high water salinities (5–10 ppt) and mangrove vegetation (*Rhizophora mangle*, *Avicennia germinans*) (Darch, 1983; Rejmankova *et al.*, 1995). Numerous small islands (<2 ha) of natural and Pre-Columbian anthropogenic origin occur in many wetlands of northern Belize (Turner, 1983). A principal focus of our research was Gold Button Lagoon (GBL; 17°5' N, 88°45' W), a 142 ha man-made impoundment located on the 10 526 ha privately owned Gold Button Ranch (GBR) in Orange Walk District. GBL contains 12 man-made islands (c. 0.125–0.5 ha) created when soil and debris were bulldozed into piles along the lagoon margin during construction in the mid-1970s; most are now heavily vegetated. Nine livestock watering ponds and Gold Button Creek provide additional crocodile habitat on GBR. Other study sites included Cox Lagoon, Sapote Lagoon, New River Lagoon, Habanero Lagoon, Laguna Seca and Laguna Verde; these are described

in greater detail elsewhere (Platt, 1996; Rainwater *et al.*, 1998; Platt & Thorbjarnarson, 2000a).

The climate of northern Belize is considered tropical with a mean monthly temperature >18 °C. Annual rainfall ranges from 1300 to 2000 mm with a pronounced wet season occurring from mid-June through late November. Average monthly precipitation is variable ranging from a maximum of 231 mm in June to a minimum of 31 mm in March (Johnson, 1983).

Methods

We conducted fieldwork during May through August 1992, May through October 1993 and 1994, and June and July 1995. We searched potential nesting habitat by foot and boat to locate crocodile nests. Although tracks and drag marks leading to nests were occasionally visible from a boat, most nests were constructed in dense vegetation and could only be located by pedestrian searches. Once identified, each nest site was revisited in subsequent years of the study. We classified nesting habitat as shoreline, natural island, man-made island or floating vegetation. Water salinity at nest sites in coastal mangrove habitat was measured to the nearest 1.0 ppt using an AtagoTM S-10E hand-held refractometer (Bellevue, WA, USA). During an initial visit to each nest we measured dimensions of the nest mound and distance to the water (measured from the center of the mound). We then carefully opened the nest, determined the clutch size, and measured (length and width to nearest 0.1 mm) and weighed (± 0.5 g) each egg. Egg viability was determined by the presence of opaque bands (Ferguson, 1985). The snout-vent length (SVL) of nesting female crocodiles was estimated from measurements of rear-foot track length (RFT) found at the nest using the equation $SVL = 6.113RFT - 5.42$ ($r^2 = 0.96$; $P < 0.001$; $n = 97$; Platt, 1996). Several nesting females were also captured and directly measured. To examine relationships between egg size and clutch size we removed the confounding effect of female body size by conducting a partial correlation analysis (Ford & Seigel, 1989; Thorbjarnarson & Hernandez, 1993; Thorbjarnarson, 1994). Residual values were generated by regressing clutch attributes on female SVL; clutch attribute residuals were then regressed against residual clutch size.

We monitored the daily nesting activity at GBR to determine the date of oviposition for each clutch. At other less-accessible sites we sacrificed a single randomly selected egg and used an embryo growth model (Platt, Rainwater & McMurry, 2003) to estimate when the clutch was deposited. Nests at GBR were inspected weekly throughout most of the incubation period; daily visits were made during the final 7–10 days. We made return visits to most nests in 1993 and 1994 to determine nesting success, defined as those nests from which at least one egg hatched. Time constraints prevented us from remaining in Belize throughout the incubation period and determining nesting success in 1992 and 1995. Tracks and other sign found at nests were used to identify predators. Following hatching, we visited the nesting areas after dusk to capture and permanently mark

neonates (Platt, Rainwater & McMurry, 2002). Rainfall data for the period of our study were obtained from the Belize Weather Bureau (Philip Goldson International Airport, Towerhill and Libertad Monitoring Stations).

Statistical references are from Zar (1996). Data were tested for violations of normality and homogeneity of variances, and if necessary log transformed to meet the assumptions of parametric tests. Proportional data were transformed using a square root arcsine transformation. Mean values are presented as ± 1 SD. Results were considered significant at $P \leq 0.05$.

Results

We found 82 *C. moreletii* nests in wetlands throughout northern Belize. One nest was found in a coastal mangrove swamp, while the remainder occurred in freshwater wetlands. Water salinity at the mangrove nest site was < 1 ppt at the time of our visit, presumably due to recent heavy rainfall. Seventy-nine (96.3%) nests were typical mound-type nests composed of vegetation (usually *Typha* or *Cladium*), soil, leaf litter and occasionally woody debris. One nest was constructed beside a snail kite *Rostrhamus sociabilis* midden and large numbers of apple snail (*Pomacea*) shells were incorporated into the mound. Nest mounds ($n = 74$) averaged 41.5 ± 10.9 cm high and 122.2 ± 28.7 cm wide. There was no correlation between mean egg width (EW) of a clutch (the best predictor of female SVL; see below) and either mound height ($r = 0.01$; $P = 0.92$; $n = 70$) or width ($r = 0.01$; $P = 0.91$; $n = 70$). Two (2.4%) nests consisted of a clutch buried in a shallow hole excavated in heavy clay soil. These two nests were found at the same site during consecutive years (1992 and 1993). Each hole measured *c.* 20 cm wide \times 25 cm deep; in 1992 the clutch was covered by a thin layer of vegetation, but the eggs were left exposed in 1993. Neither clutch proved viable. Owing to the similarity in the mean EW of both clutches, we believe these nests were constructed by the same female. Finally, one clutch (1.2%) was buried in a detritus mound at the base of a cohune palm *Orbigyna cohune*. In this instance the female deposited eggs in a pre-existing mound of decomposing palm fronds and other debris without modification.

We found one nest (1.2%) on a floating mat of vegetated peat (considered a natural island in our analyses of nesting success below); all other nests were constructed on solid substrates. Despite considerable searching, we did not find nests in cattail (*Typha*) beds, among floating vegetation, or on other unstable substrates. Forty-seven (57.3%) nests were found on islands, and 35 (42.6%) were constructed along a continuous shoreline. Island nests were constructed closer to water (5.6 ± 5.0 m; range = 0.3–20.0 m) than shoreline nests (6.6 ± 4.9 m; range = 1.0–17.0 m), although this difference was not significant ($F_{3,71} = 0.61$; $P = 0.43$). There was no correlation between mean EW of a clutch and the distance of nests to water ($r = 0.02$; $P = 0.82$; $n = 70$). In general, nest mounds constructed primarily of vegetation deteriorated rapidly and were indiscernible by the following nesting season; however, mounds composed of soil and leaf

litter often remained intact for more than 1 year. We found ants (Hymenoptera) in 10 (12.1%) nests, termites (Isoptera) in four (4.8%) nests and the eggs of a basilisk lizard *Basiliscus vittatus* in one (1.2%) nest. During the dry season Neotropical sliders *Trachemys scripta venusta* frequently deposited clutches at sites later used by nesting *C. moreletii* in the wet season, but we found no turtle eggs in active crocodile nests.

Nesting activity commenced at the onset of the wet season in mid- to late June and continued into mid-July (Fig. 1). We frequently noted fresh crocodile tracks and scrapings at nest sites 24–48 h after the first heavy rainfall of the season; oviposition followed in 5–7 days. The mean date of laying was 1 July ± 10 days (range = 22 May to 18 July; $n = 68$); this did not differ significantly among years ($F_{3,64} = 0.89$; $P = 0.45$). There was no correlation between date of oviposition and mean EW of a clutch ($r = 0.11$; $P = 0.35$), clutch size ($r = 0.073$; $P = 0.546$) or clutch mass ($r = 0.085$; $P = 0.485$). We were able to determine hatching dates for 12 clutches; the mean date of hatching was 14 September (range = 17 August to 14 October) and the mean incubation period was 75 ± 11 days (range = 61–100 days).

We often found nests at the same location each year, although their exact position tended to vary within a few meters. Female crocodiles also occasionally added new material and reused nest mounds persisting from previous years. Of the nest sites we located in 1992, one was used consecutively for 4 years, another for 3 years and two for 2 years. We were unable to determine whether the same or different females were responsible for repeated use of these nest sites.

Because it is likely that some nests escaped detection, we could not make meaningful comparisons of annual nesting effort at most study sites. However, an intensive search effort and our familiarity with GBR allowed us to locate all nests at this site during each year of the study. Nesting effort remained relatively constant during 1992, 1993 and 1995, but nearly doubled in 1994 (Fig. 2).

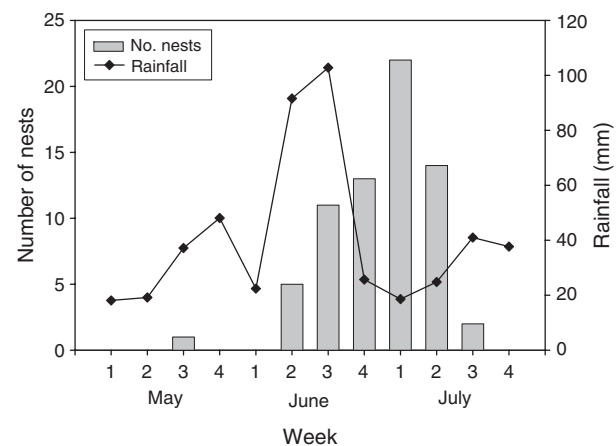


Figure 1 Timing of clutch deposition by *Crocodylus moreletii* ($n = 68$) in relation to mean rainfall (1992–1995) in northern Belize. Rainfall data from Belize Weather Bureau.

Of the 82 *C. moreletii* nests that we found, 72 (87.8%) contained eggs (Table 1). Additionally, we removed a clutch of partially shelled oviducal eggs from a female *C. moreletii* that drowned in a fishing net. Mean clutch size was 25.0 ± 7.6 (range = 9–42; $n = 73$) and did not differ significantly among years ($F_{3,69} = 0.65$; $P = 0.58$). We measured the linear dimensions of 1722 eggs (including 20 eggs from which the contents had leaked); mean length and width were 68.8 ± 4.1 mm (range = 57.0–98.2 mm) and 41.1 ± 1.8 mm (range = 35.4–49.0 mm), respectively. Mean egg mass (EM) was 69.0 ± 9.4 g (range = 46.2–91.1 g; $n = 1702$) and differed significantly among years ($F_{3,1698} = 9.47$; $P < 0.005$). Mean EM in 1992 and 1994 was significantly greater than EM in 1993 and 1995 (Tukey–Kramer MSD; $P < 0.05$). EM was predicted from both egg length (EL) and EW by the equation $EM = 2.93EW + 1.12EL - 129.08$ ($r^2 = 0.92$; $P < 0.001$; $n = 1702$). Clutch mass ranged from 579.5 to 3646.0 (mean = 1693.7 ± 621.7 g; $n = 68$).

One hundred and forty-eight (8.7%) of 1702 intact eggs we examined were non-viable. The proportion of non-viable eggs differed significantly among years ($\chi^2 = 30.98$, d.f. = 3, $P < 0.001$), and was greatest in 1993 and 1995 (Table 1). There was no correlation between the proportion of non-viable eggs (data arcsine transformed) and date of oviposition ($r = 0.091$; $P = 0.45$) or clutch size ($r = 0.166$; $P = 0.17$).

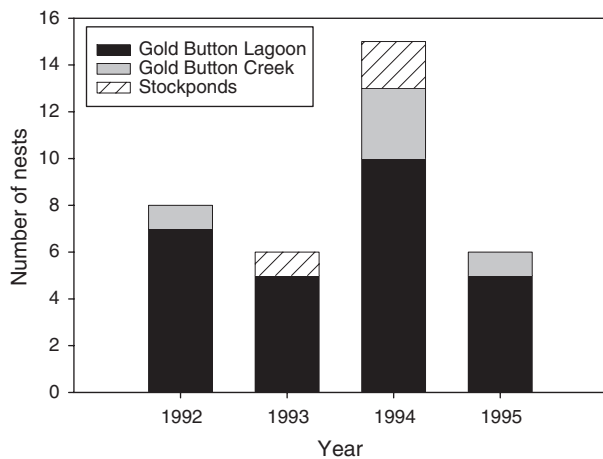


Figure 2 Nesting effort of Morelet's crocodiles on Gold Button Ranch, Belize (1992–1995).

A marginally significant and perhaps biologically meaningful correlation was found between the proportion of non-viable eggs and mean EW of the clutch ($r = -0.22$; $P = 0.06$).

We directly measured the SVL of five females captured at nests, estimated the SVL of 10 females from rear-foot tracks found at nests, and recovered a gravid female that drowned in a fishing net ($n = 16$). There was a significant positive correlation between female SVL and clutch size, clutch mass, mean EM, mean EW and mean EL (Fig. 3). Log transforming these variables as recommended by King (2000) failed to improve the fit of our regression models. Mean EW was the best predictor of female SVL ($SVL = 5.42EW - 132.6$; $r^2 = 0.68$; $P < 0.001$). A partial correlation analysis of egg and clutch attributes indicated that independent of female SVL, there was a significant positive relationship between clutch size and mean EM, mean EL, and clutch mass, and a positive, although non-significant relationship between clutch size and mean EW (Table 2).

The SVL of the 16 females that we directly measured or estimated from tracks found at nests ranged from 77.0 to 112.0 cm (TL *c.* 148.0–214.2 cm, respectively). We used EW from individual clutches to estimate the SVL of 57 other females, which ranged from 64.4 to 108.9 cm (TL *c.* 121–209 cm, respectively). After pooling the two datasets, the estimated mean SVL of nesting females ($n = 73$) was 88.9 ± 9.7 cm (TL *c.* 171 cm) with a range of 64.4–112.0 cm (TL *c.* 121–214.2 cm, respectively) (Fig. 4). There was no significant difference in the mean SVL of nesting females among years ($F_{3,69} = 0.43$; $P = 0.73$).

During the 1993 and 1994 nesting seasons, 30 (50.8%) nests were successful and produced at least one viable hatchling, 26 (44.0%) were unsuccessful, and the fate of three (5.0%) could not be determined (Table 3). Overall nesting success did not differ significantly among years ($\chi^2 = 0.06$; d.f. = 1; $P < 0.05$). Of the 26 unsuccessful nests, most losses were attributable to flooding (27.0%) and predation (61.5%). There were no significant differences in nest losses due to flooding among years ($\chi^2 = 2.10$; d.f. = 1); however, losses from predation were significantly greater in 1994 than in 1993 ($\chi^2 = 4.74$; d.f. = 1; $P < 0.05$). Additionally, complete clutches in three (11.5%) nests failed to develop or died during incubation. One of these clutches was laid almost a month before the wet season began, and the well-developed embryos perished when eggs desiccated.

Table 1 Clutch attributes and estimated snout–vent length (SVL) of nesting female *Crocodylus moreletii* in northern Belize (1992–1995)

Parameter	1992	1993	1994	1995
Clutch size	27.8 ± 7.6 (10) ^a	25.6 ± 7.7 (15)	24.3 ± 8.1 (38)	23.8 ± 5.6 (10)
Egg length (mm)	69.9 ± 3.4 (236)	68.4 ± 4.0 (378)	69.0 ± 4.1 (870)	68.0 ± 4.7 (238)
Egg width (mm)	41.3 ± 1.5 (236)	40.9 ± 1.8 (378)	41.3 ± 1.9 (870)	40.3 ± 1.9 (238)
Egg mass (g)	69.7 ± 8.4 (236)	67.9 ± 8.4 (367)	69.8 ± 9.7 (863)	66.6 ± 9.9 (236)
Clutch mass (g)	1830.2 ± 710.2 (9)	1709.8 ± 496.9 (15)	1706.3 ± 700.4 (38)	1586 ± 416.0 (10)
Non-viable eggs (%)	5.1	14.4	6.1	12.6
Female SVL (cm)	90.3 ± 8.2 (10)	89.7 ± 7.2 (15)	89.9 ± 7.6 (38)	87.4 ± 11.0 (10)

Where appropriate, values presented as mean \pm 1 sd (n).

^aIncludes clutch of partially shelled oviducal eggs removed from a dead female.

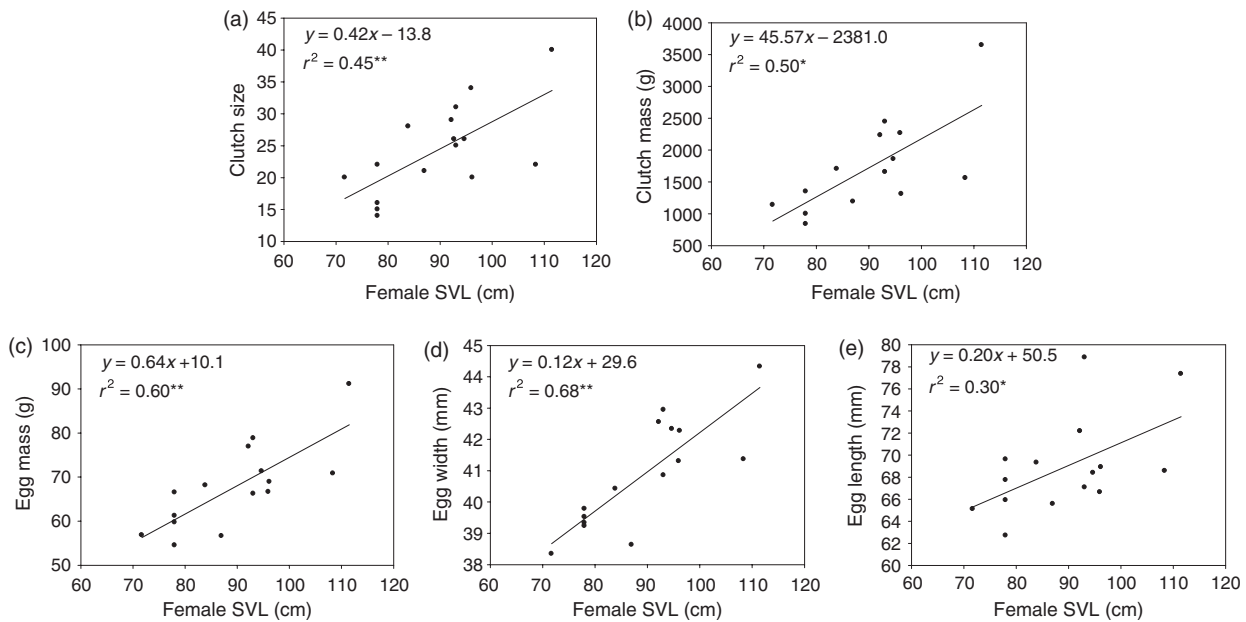


Figure 3 Relationship between the snout–vent length (SVL) of female *Crocodylus moreletii* and (a) clutch size, (b) clutch mass, (c) mean egg mass, (d) mean egg width, (e) mean egg length (* $P < 0.05$; ** $P < 0.001$).

Table 2 Partial correlation coefficients between residual clutch size and residual values of the reproductive parameters indicated

Parameter	r	n
Clutch mass	0.92**	14
Egg mass	0.55*	15
Egg width	0.44 NS	15
Egg length	0.54*	15

Residuals were generated by regressing reproductive parameters against female SVL.

* $P < 0.05$.

** $P < 0.001$.

NS, not significant; SVL, snout–vent length.

Nesting success was not independent of nesting habitat ($\chi^2 = 14.15$, d.f. = 2, $P < 0.001$; Table 4). Nesting success was significantly greater on natural islands in comparison to man-made islands ($\chi^2 = 7.53$; d.f. = 1; $P < 0.05$) or nests constructed along the shoreline ($\chi^2 = 21.37$; d.f. = 1; $P < 0.05$). Nesting success among shoreline nests and those constructed on man-made islands did not differ significantly ($\chi^2 = 0.96$; d.f. = 1; $P > 0.05$).

We determined that raccoons *Procyon lotor* were responsible for most nest predation. Raccoons often made repeated visits to a nest, removing a few eggs each time. Collared peccary *Tayassu tajacu* destroyed one nest, and rice rats (*Oryzomys* sp.) consumed 19 eggs from a clutch of 29, although 10 eggs eventually hatched. Most nest predation occurred in 1994 (Table 3), and peaked during early August when water levels were unseasonably low.

Our weekly nest inspections at GBR indicated that adult crocodiles, presumably nesting females, made frequent visits to nests throughout the incubation period. We often noted

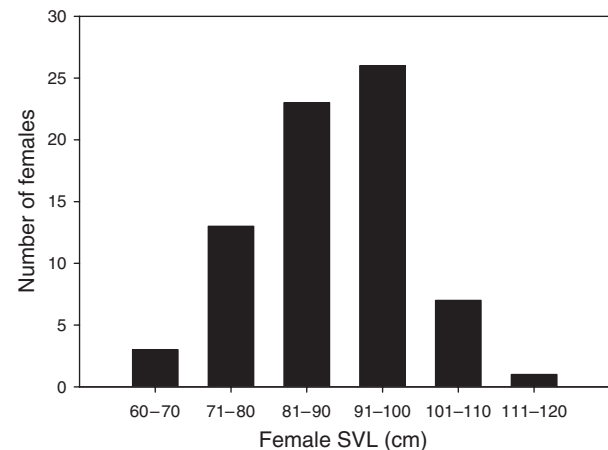


Figure 4 Size-class distribution of 73 nesting female *Crocodylus moreletii* in northern Belize (1992–1995). Snout–vent length (SVL) was determined from measurements of nesting females ($n = 6$), or estimated from the length of tracks found at nest sites ($n = 10$) or mean egg width of clutches ($n = 57$).

fresh mud smears atop nests, and found drag marks and scrapings in the vicinity. In several instances females repaired damaged nest mounds following predator visitations. Although females were frequently observed near nests, aggressive nest defence behavior was noted only twice. During these encounters, females hissed loudly, and repeatedly charged us.

Of the 30 successful nests, 24 (80%) were opened by females to liberate hatchlings. At GBL females opened nests 12–24 h after we noted hatchlings beginning to vocalize from within the mound. Tracks and eggshells found at opened

nests indicated that females transported neonates from the nest to water. We found six nests that females failed to open; three contained colonies of ants which killed and partially consumed all of neonates after hatching. In two other nests composed primarily of soil, 20 of 29 and nine of 17 neonates were killed by ants; empty eggshells suggested that the remaining neonates managed to exit the mound unassisted by the female. Likewise, hatched eggs found in another nest indicated that 10 neonates emerged unassisted from the mound of *Typha* after the rest of the clutch was consumed by rice rats.

We captured and marked 106 neonates during 1993 and 1994. Mean hatchling morphometric measurements were: SVL = 13.0 ± 0.5 cm (range = 11.5–14.1 cm); TL = 26.9 ± 1.3 cm (range = 23.9–29.5 cm); mass = 50.2 ± 5.0 g (range = 40.5–59.5 g). Neonates formed pods and remained concealed among aquatic vegetation, particularly *Eleocharis* in the vicinity of nest sites. Based on observations of groups composed of similar-sized individuals and estimated size-age relationships, we speculate that pods may remain intact for up to 2 years. We frequently observed neonates in the company of adults, and the latter often responded aggressively to distress vocalizations made by neonates when being captured.

Discussion

Nest and nest site characteristics

We consider earlier reports that *C. moreletii* constructs hole nests (Greer, 1970; Campbell, 1972b; Brazaitis, 1973) erroneous; these probably resulted from confusion with the morphologically similar and broadly sympatric *Crocodylus acutus* (Platt & Rainwater, 2005), a hole-nesting crocodilian that nests from March to early May in Belize (Platt & Thorbjarnarson, 2000b). The two hole nests we found at GBL are thought to represent anomalous, maladaptive behavior as neither proved viable and, moreover, clutches deposited belowground during the wet season would be prone to flooding. It is also possible these nests represent the efforts of a *C. moreletii* × *acutus* hybrid. The two species occasionally hybridize in Belize (Ray *et al.*, 2004), but the limited data available suggest hybrids nest during the dry season and deposit clutches in large sand mounds rather than holes (Platt & Thorbjarnarson, 1997). Interestingly, Hayes-Odum *et al.* (1994) reported a similar hole nest constructed by the normally mound-nesting *Alligator mississippiensis*.

According to Alvarez del Toro (1974) there is a positive relationship between nest size and female body size, that is, larger females construct the largest nest mounds. This is contrary to our findings in Belize where the size of the nest mound appeared to reflect the type and availability of materials at the nest site. In general, the largest nest mounds were constructed of *Typha* and *Cladium*. However, *Typha* mounds tend to decrease in size as the nesting season progresses owing to the rapid decomposition of this succulent plant material.

Our study was the first to document nesting of *C. moreletii* in coastal mangrove habitats. While earlier reports (Neill, 1971; Campbell, 1972a) suggested *C. moreletii* was restricted to freshwater wetlands, others noted the occurrence of *C. moreletii* in mangroves, but found no evidence of nesting (Powell, 1965; Abercrombie *et al.*, 1980; Meerman, 1992; Cedeño-Vázquez, Ross & Calmé, 2006). Although the salinity tolerance of hatchling *C. moreletii* is unknown and potentially limiting in coastal wetlands, hatching occurs in the mid-wet season, a period when salinities are reduced by an influx of freshwater into mangrove ecosystems (Zisman, 1992).

Nest site selection remains one of the least understood aspects of crocodilian nesting ecology (Lang, 1987). Not surprisingly, little is known regarding nest site selection by *C. moreletii* and few published descriptions of nest sites are available. Alvarez del Toro (1974) stated that nests are constructed on 'elevated' sites, often a considerable distance from water, and Perez-Higareda (1980) described a single nest constructed 'over an accumulation of aquatic lilies . . . in water, not on firm land.' With one exception, the *C. moreletii* nests that we found in Belize were constructed on solid substrates, and never on muck or among aquatic vegetation where the risk of flooding would be great. Other crocodilians frequently nest on floating vegetation, which rises and falls with changing water levels and offers protection from flooding (Webb *et al.*, 1983b; Hall & Johnson, 1987; Campos, 1993). While floating peat provides a suitable nesting substrate in Belize, it occurred at only two of >60 wetlands we surveyed. Other types of floating vegetation in northern Belize (e.g. *Panicum* sp.) appear incapable of supporting the weight of an adult crocodile or its nest.

The position of *C. moreletii* nests relative to water varied considerably in northern Belize. Nest positioning probably reflects a balance between placing the nest far enough from water to minimize the risk of flooding, yet close enough for adults to guard (Cintra, 1988). Where available, both man-made and natural islands are heavily used as nesting sites by

Table 3 Summary of nesting success and causes of nest failure among *Crocodylus moreletii* nests in northern Belize (1993 and 1994)

Year	Unsuccessful nests			Total lost	Successful nests	Fate unknown	Total nests
	Flooding	Predators	Other				
1993	3 (18.7)	2 (12.5)	2 (12.5)	7 (43.7)	9 (56.2)	0	16
1994	4 (9.3)	14 (32.5)	1 (2.3)	19 (44.1)	21 (48.8)	3 (6.9)	43
Total	7 (11.8)	16 (27.1)	3 (5.0)	26 (44.0)	30 (50.8)	3 (5.0)	59

Values in parentheses are per cent of row or column total.

Table 4 *Crocodylus moreletii* nesting success in northern Belize summarized by habitat (1993 and 1994)

Habitat	Unsuccessful nests			Successful nests	Total
	Flooding	Predators	Total		
Shoreline	3 (12.5)	13 (53.)	16 (66.6)	8 (33.3)	24
Natural islands	0	1 (5.8)	1 (5.8)	16 (94.1)	17
Man-made islands	4 (33.3)	2 (16.6)	6 (50.0)	6 (50.0)	12
Total	7 (13.2)	16 (30.1)	23 (43.3)	30 (56.6)	53

Values in parentheses are per cent of row or column total. Two shoreline nests that contained only non-viable eggs are not included.

C. moreletii in Belize. Likewise, female *A. mississippiensis* exhibit a similar preference for small islands as nesting sites (Hayes-Odum *et al.*, 1993).

Reproductive phenology

Considerable ambiguity surrounds the timing of nest construction and clutch deposition in *C. moreletii*. Powell (1972) and Alvarez del Toro (1974) stated that nesting occurs from April to June in Mexico, but neither provided specific data. Likewise, captive *C. moreletii* of Mexican provenance held by zoological collections in the United States reportedly nest in May and June (Hunt, 1973, 1980). Similar to our observations in Belize, Casas-Andreu & Rogel-Bahena (1986) found that *C. moreletii* in southern Mexico nest during June and July, a period that coincides with the beginning of the wet season in both regions. Nesting among crocodilians occurs when moisture and temperature regimes are synchronized (Webb & Cooper-Preston, 1989), and may change over latitudinal gradients in response to local environmental conditions (Thorbjarnarson, 1989). Given that oviposition in crocodilians generally occurs 20–30 days after ovulation (Lance, 1987; Astheimer, Manolis & Grau, 1989), courtship among *C. moreletii* in Belize is thought to take place late in the dry season (April–May).

Birth pulse and birth flow models (Caughley, 1977) have been used to describe the temporal distribution of clutch deposition among nesting crocodilians (Hall, 1991). The temporally compressed nesting and oviposition period that we describe for *C. moreletii* is consistent with a birth pulse model as the 10 day SD of egg laying in Belize is within the range of the 30 day SD of this model. A larger SD would be consistent with a birth flow model. *Crocodylus moreletii* is unusual in this regard, as most tropical, mound-nesting crocodilians exhibit a birth flow strategy and nest over an extended period during the wet season (Hall, 1991).

The proximal cue for nesting appears to be the heavy rains that herald the onset of the wet season. Nesting after the peak rainfall of mid-June probably allows females to position nests above the normal high-water mark and minimize clutch mortality from flooding. Conversely, nesting before the wet season could result in egg desiccation if nest material dries (Joanen & McNease, 1989). Indeed, the only instance of dry season nesting that we observed was unsuccessful for this reason.

The selective advantage of a temporally compressed nesting season is less clear, but may be related to seasonal fluctuations in water level. Survival of neonate crocodilians is enhanced under flooded conditions (Staton & Dixon, 1977), and nesting early in the wet season insures that hatching occurs when water levels are elevated, thereby allowing neonates ready access to flooded vegetation that provides important escape cover and harbors a diverse array of invertebrate prey (Platt *et al.*, 2002). Moreover, nesting at the beginning of the wet season maximizes the time neonates can remain in favorable habitat before the onset of more stressful dry season conditions (Allsteadt, 1994). Thermal constraints on nesting are probably less important as monthly variation in air temperature is minimal in northern Belize except during the winter months (Johnson, 1983).

Size of nesting females

Virtually nothing is known regarding the size distribution or size/age at sexual maturity of female *C. moreletii*. According to Casas-Andreu & Rogel-Bahena (1986) and Hunt (1980), the average TL of small groups of nesting females ranged from 219 cm ($n = 9$) to 225 cm ($n = 7$), respectively, and Perez-Higareda (1980) encountered a 300 cm TL female guarding a nest; the latter is probably close to the maximum size attained by female *C. moreletii*. The mean TL of nesting female *C. moreletii* in Belize was considerably less than described in these earlier reports. Furthermore, our observations of nesting females measuring < 150 cm TL suggests that sexual maturity is attained at about 50% of maximum adult female body length. Based on preliminary growth data, 7–8 years are probably required for females to reach sexual maturity (Platt, 1996).

Nesting effort

Our observations at GBR indicate that the number of female *C. moreletii* nesting in 1994 almost doubled in comparison to other years of the study. This increase was unlikely due to a change in population as the number of crocodiles counted during spotlight surveys remained stable during the 4 years of our study (Platt, 1996). Moreover, increased nesting effort at GBR appeared to reflect a regional trend observed throughout northern Belize in 1994; that is, we found a greater number of nests at most sites than in other years of the study. Similar variation in

annual nesting effort among other crocodylians (e.g. Joanen & McNease, 1989; Taylor, Kinler & Linscombe, 1991; Hayes-Odum *et al.*, 1993; Thorbjarnarson, 1994) is thought to be the result of a complex and poorly understood interaction between environmental, nutritional and physiological factors (Nichols, 1989; Kushlan & Jacobsen, 1990). We speculate that a much greater proportion of female *C. moreletii* nested in 1994 than in other years of the study because heavy rains at the beginning of the 1993 season flooded many nesting sites and possibly caused some females to postpone reproduction until the following year. Moreover, elevated water levels through much of the 1993–1994 dry season may have allowed females greater access to flooded vegetation and other high-quality foraging habitats (Platt *et al.*, 2006), thereby reducing drought-related nutritional stress that could affect clutch production (Kushlan & Jacobsen, 1990).

Parental attendance

The presence of females near nests, tracks at the nest site, restoration of damaged nests and obvious signs of nest opening to liberate neonates upon hatching strongly suggest that females attend nests throughout the incubation period. Moreover, observations of females and in one instance a large male (Rainwater, McMurry & Platt, 2000) responding to neonate distress vocalizations suggest that parental attendance among *C. moreletii* continues after hatching and may not be limited to females. Likewise, Hunt (1980) observed both female and male *C. moreletii* attending neonates in captivity. The few instances of aggressive behavior directed toward us are considered a poor index of general behavior, as females may selectively avoid humans, but still defend against smaller predators (Hunt & Ogden, 1991). Furthermore, responses of crocodylians toward humans often reflect a past history of hunting, which is thought to have curtailed nest defence behavior in exploited populations (Crawshaw, 1991). This may be the case in northern Belize where it was once common practice for hunters to lure adult crocodiles into gunshot range by imitating the distress calls of hatchlings (Platt, 1996).

Nesting success

Our results are consistent with other studies of mound-nesting crocodylians that attribute most clutch mortality to a combination of flooding and predation, with minor losses from other factors such as unsuitable thermal regimes and egg desiccation (Magnusson, 1982; Hall & Johnson, 1987; Hunt & Ogden, 1991; Campos, 1993; Allsteadt, 1994).

Crocodylian eggs are intolerant of flooding, and submergence for more than 12 h results in embryo death (Joaen, McNease & Perry, 1977). Hall (1991) speculated that female crocodiles cue on high-water marks from previous years and construct nests above that point. We found nothing to suggest this occurs among *C. moreletii*; indeed, nests were often constructed on sites that flooded during previous nesting seasons. Flooding is unpredictable in Belize, espe-

cially in alluvial habitats (Platt & Thorbjarnarson, 2000a) and any fitness advantage gained by placing a nest well above the limit of potential flooding may be negated by an increased likelihood of predation.

Similar to other studies that noted intense nest predation during periods of low water levels (Fleming, Palmisano & Joanen, 1976; Hunt & Ogden, 1991; Larriera & Piña, 2000), most predation of *C. moreletii* nests occurred during an unseasonably dry period midway through the 1994 nesting season. Low water levels at this time allowed predators easy access to nests, particularly those on man-made islands no longer isolated from the mainland by open water. Furthermore, the lack of sufficiently deep water near nests appeared to discourage female attendance and nest guarding behavior. Others have demonstrated that unattended crocodylian nests suffer disproportionately high levels of predation (Dietz & Hines, 1980; Hunt & Ogden, 1991).

Ants were responsible for hatchling mortality only at *C. moreletii* nests that the attending female failed to open. Although ant colonies are frequently found in crocodylian nest mounds (Staton & Dixon, 1977; Platt, Hastings & Brantley, 1995), their effect on hatchling fitness is complex and not well-studied. Ants may discourage females from opening nests and kill hatchlings (Reagan, Ertel & Wright, 2000), but on the other hand act as cleaning agents to rid nests of fungal growth and rotten eggs, deter nest predators, and maintain favorable temperature and humidity regimes within the nest mound (Riley, Stimson & Winch, 1985).

Similar to studies of other mound-nesting crocodylians (Jennings, Percival & Abercrombie, 1987; Campos, 1993), we found that nesting habitat strongly influences nesting success among *C. moreletii* in Belize. Nesting success was greatest on islands, particularly natural islands, while losses were highest among nests constructed along shorelines. We attribute this to several factors. First, shorelines are in effect linear edge habitats where nest predation rates are typically high (Lahti, 2001). Second, islands preclude ready access by predators, which risk attack by attending females while crossing deep or open water. Third, flooding of natural islands rarely occurs because ground water reservoirs act as sinks for excessive rainfall, dampening water level fluctuations in natural wetlands (Johnson, 1983). However, in contrast to natural wetlands, pronounced water-level fluctuations occurred at GBL following heavy rains, resulting in occasional nest flooding on man-made islands.

Clutch characteristics

The clutch size of *C. moreletii* in northern Belize is comparable to the range of 20–42, but somewhat less than the mean of 30.3 ± 13.5 (range = 11–51; $n = 8$) reported by Alvarez del Toro (1974) and Casas-Andreu & Rogel-Bahena (1986), respectively. Perez-Higareda (1980) found a clutch of 70 eggs in a *C. moreletii* nest, and while this could represent the reproductive efforts of more than one female (e.g. Enge *et al.*, 2000), the uniform egg size, large mean EL (100 mm) and presence of a large (TL = 3.0 m) attending female

suggest this clutch was produced by a single female. Seventy eggs is likely the near-maximum clutch size for *C. moreletii*.

While generally low, the percentage of non-viable *C. moreletii* eggs was greatest during years of climatic extremes. We speculate that females experienced increased stress levels during these periods, ultimately leading to a decline in egg viability. Unusually heavy rains during the peak nesting period of 1993 flooded many partially completed nest mounds forcing females to delay oviposition for 1–2 weeks while new mounds were constructed. In 1995, a severe drought before the nesting season concentrated crocodiles in drying wetlands and likely increased aggressive interactions between dominant and subdominant individuals. Female crocodilians subjected to stressful conditions often retain oviducal eggs for longer than normal periods (Ferguson, 1985), causing viability to decline when extra calcium is deposited on the eggshell, thus reducing porosity and hence gas exchange (Wink, Elsey & Bouvier, 1990).

Clutch and egg size increase with female body size in many reptiles (Ford & Seigel, 1989), although this relationship is highly variable both inter- and intraspecifically among crocodilians (Thorbjarnarson, 1996). Similar to our findings, Alvarez del Toro (1974) stated that 'younger' (and presumably smaller) female *C. moreletii* lay small eggs; however, Casas-Andreu & Rogel-Bahena (1986) found no correlation between female body size and clutch size, mean EW or clutch mass ($n = 7$).

Theoretical models of optimal clutch size predict an inverse relationship between clutch size and EM because energy allocated to reproduction must be divided among both (Brockelman, 1975; Stearns, 1992). However, few studies of reptiles have detected this relationship because statistical procedures that hold female body size constant while testing the effect of clutch size on offspring or egg size, have rarely been used (Ford & Seigel, 1989).

Evidence for a trade-off between clutch size and EM in crocodilians has not been forthcoming. Thorbjarnarson & Hernandez (1993) found clutch size, egg size and clutch mass were positively correlated with female body size in *C. intermedius*, but when female size was held constant, there was no trade-off between clutch size and egg size. Likewise, Thorbjarnarson (1994) reported that clutch size and clutch mass, but not EM, were positively correlated with female body size in *Caiman crocodilus*; however, independent of female size, increases in clutch size were not accompanied by increases in EM or width, although a decrease in EL was noted, probably in response to linear egg placement within the oviduct. Larriera *et al.* (2004) found that clutch size and EM were positively correlated with female body size in *Caiman latirostris*, but these relationships were not independent of body size.

As in studies of other crocodilians, we found no evidence for a trade-off between clutch size and egg size in *C. moreletii*. Instead, our partial correlation analyses of clutch attributes indicate that after controlling for female SVL, EM increases with increasing clutch size, a finding inconsistent with optimal clutch size theory. According to Van Noordwijk & de Jong (1986), observations of positive

correlations between life history traits when trade-offs, and hence negative correlations are expected, are thought to occur when the fraction of total energy allocated to reproduction varies among individuals in a population. Individuals can increase both the number and size of offspring by increasing the fraction of the overall energy budget allocated to reproduction, even while total energy expenditure remains constant.

Our results suggest that female *C. moreletii* are allocating energy to increase both clutch size and EM, that is, larger clutches consist of larger eggs than would be predicted by female SVL alone. Among crocodilians, the energy available for reproduction increases as females mature owing to a reduction in energetic demands for growth and a concomitant increase in the lipid storage capacity of larger individuals (Thorbjarnarson, 1996). Additionally, allometric changes in skull morphology provide larger crocodiles access to an expanded prey base (Hall & Portier, 1994), and larger, dominant females may restrict access of subdominants to resources through competitive interactions (Lang, 1987). Furthermore, the resource base available to female crocodiles at our primary study site (GBL) is extraordinarily rich; in addition to abundant natural prey, crocodiles have occasional access to cattle carcasses (Platt *et al.*, 2007).

The increase in EM that accompanies increasing clutch size in *C. moreletii* is the result of increases in EL. EW is not independent of female body size in crocodilians, and probably constrained by the pelvic aperture diameter (Thorbjarnarson, 1994; Larriera *et al.*, 2004). Likewise, among some lizards, EW is highly conserved, while EL varies considerably (Werner, 1989). These species circumvent rigid pelvic girdle constraints by producing longer eggs, although functional limitations to EL do exist (Sinervo & Licht, 1991).

A basic assumption of optimal clutch size models is that neonatal fitness is positively related to body size (Lloyd, 1987; Stearns, 1992; Bernardo, 1996). Large neonatal body size is thought to favor avoidance or escape from potential predators, accelerated growth, greater foraging efficiency and increased thermoregulatory abilities (Sinervo, 1990; Stearns, 1992). Among crocodilians hatchling size is correlated with egg size (Staton & Dixon, 1977; Dietz & Hines, 1980; Webb *et al.*, 1983a; Larriera *et al.*, 2004), but the extent to which hatchling size affects fitness remains unresolved (Webb & Cooper-Preston, 1989). Indeed, the lack of ecological studies makes the adaptive significance of larger neonatal body size in crocodilians highly speculative at best (Allsteadt & Lang, 1995). In contrast to most vertebrates in which offspring fitness is determined solely by parental investment (Bernardo, 1996), in crocodilians incubation temperatures affect a suite of hatchling attributes in addition to sex (Deeming & Ferguson, 1989), leading Thorbjarnarson (1994) to suggest that factors associated with environmental sex determination act to uncouple the relationship between egg size and neonatal fitness. However, Piña *et al.* (2007) noted clutch-specific effects in the size of hatchling *C. latirostris* incubated at different temperatures, and Allsteadt & Lang (1995) found strong clutch effects and

significant temperature-by-clutch interactions on most hatchling parameters in *A. mississippiensis*. Collectively, these results indicate that genetic and/or maternal effects, in addition to incubation temperatures, are likely important determinants of neonatal fitness. Clearly the relationship between neonatal body size and fitness warrants further investigation among *C. moreletii* and other crocodylians.

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