

Reproductive ecology of Orinoco crocodiles (*Crocodylus intermedius*) in a newly established population at El Frío Biological Station, Venezuela

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We present data on the reproductive ecology of the Orinoco crocodile (*Crocodylus intermedius*) in a newly established population at the El Frío Biological Station, Venezuela, from 2003 to 2007. Nesting occurs during the dry season, and hatching of young takes place at the beginning of the rainy season. Elliptical hole-like nests are constructed in artificial sand beaches with a median nest depth of 42.6 cm. Nest depth is positively correlated with female total size, enabling us to predict the size of the female based on nest characteristics. Temperature in the egg chamber was on average 31.9 °C. The thermal amplitude of the nest was positively correlated with nest depth, and less than 1.3 °C when the nest was deeper than 30 cm. The average clutch size was 41.2 eggs, the average clutch mass was 4256.2 g, and egg viability was 75.4%. The average length, width and weight of eggs was 7.61 cm, 4.73 cm and 111.07 g, respectively. As part of the conservation programme, we also artificially incubated eggs from the species. Hatching rate in the incubator was 84.3%. Total length and mass at hatching were 28.6 cm and 66.9 g, respectively. Our data demonstrate that head-starting our population through egg incubation is a suitable conservation strategy for this endangered species.

Key words: conservation, head-starting, management, reintroduction

INTRODUCTION

The Orinoco crocodile (*Crocodylus intermedius*) is one of the most endangered and least studied New World crocodylians (Ross, 1998). Gumilla (1745) was the first to provide information about courtship and mating chronology, nesting and parental care in Venezuela. Medem (1958, 1981, 1983) described nesting chronology, clutch size, egg dimensions, nest temperatures and reproductive behaviour in Colombia, the second country where the species occurs. Because of its rarity and its threatened status, Orinoco crocodile captive breeding programmes were developed and provided further information about captive reproduction (Ramírez et al., 1977; Ramo et al., 1992; Thorbjarnarson & Hernández, 1993a,b; Seijas, 1994, 1995; Lugo, 1995; Colvée, 1999; Ramírez-Perilla & Urbano, 2002). Since the 1990s, several studies have also been conducted to determine the status of wild populations, mainly in Venezuela (Cojedes river system: González-Fernández, 1995; Seijas & Chávez, 2002; Ávila-Manjón, 2008; Capanaparo river: Thorbjarnarson & Hernández, 1993a,b; Manapire River: Jiménez-Oraá et al., 2008).

Here we present, for the first time, reproductive data over a five-year period on a newly established Orinoco crocodile population in the El Frío Biological Station, Caño Wildlife Refuge, and surrounding areas, founded by introducing subadult crocodiles raised in captivity (Antelo, 2008). The introduction programme started in 1990, and reproduction was first observed in 1996. We also provide information about a head-starting pro-

gramme during which eggs are collected from wild nests and incubated, and subadult crocodiles are released once they have reached a total length of 80 cm after about one year.

STUDY AREA AND METHODS

The study was conducted at the El Frío Biological Station (7°38'–7°53'N; 68°43'–69°03'W), a private 62,000-ha protected area located in southwest Venezuela in the heart of the flooded llanos (Velasco & Ayarzagüena, 1995). The study area can be characterized as a tropical wet savannah with a well defined wet season between April and November, and a dry season between December and May. During the wet season, 80% of the area is flooded, while during the dry season landscapes become dry and water is restricted to a few *caños* (seasonal running water) and lagoons.

The study was carried out through five consecutive breeding seasons (2003–2007); in 2007 the field work terminated at the beginning of March. Territorial, courtship and mating behaviour was also studied in a pair of captive adult crocodiles in the Station. The onset of the breeding season was determined by the observation of loud roars emitted by adult males that have been described as indicators of territoriality and courtship (Medem, 1981; Thorbjarnarson & Hernández, 1993b; Colvée, 1999; Antelo, 2008). The Orinoco crocodile nests on river banks and beaches that are exposed during the dry season. Most water bodies in the study area lack a sandy substrate, and the compact clay soil makes nest digging

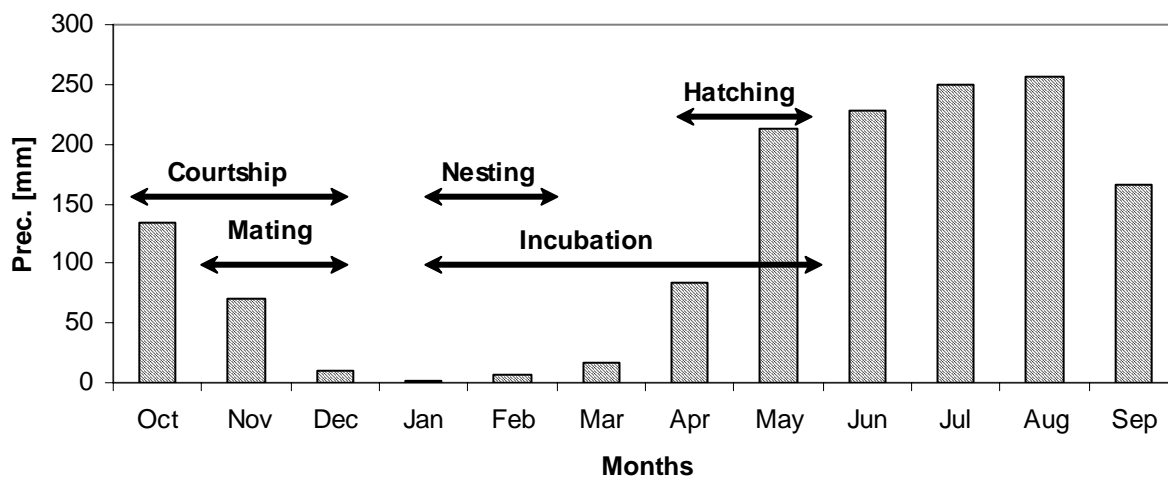


Fig. 1. Annual pattern of precipitation in Hato Cañafístolo (18 km northwest of EFBS) related to reproductive events in the Orinoco crocodile; the data shown are means between 1969 and 2003.

difficult and prevents water infiltration. For this reason, since 1999 we have provided 1–2 m³ sand mounds in areas used by females to lay their eggs during the second week of January. Wind and the breeding females expand the sand and turn it into a small beach. Around 10 artificial beaches are deposited every year, mostly on the banks of the Caño Macanillal and the La Ramera lagoon, and also at the Los Españoles lagoon.

In order to avoid egg-predation, egg searching started immediately after depositing the mounds of sand, based on body marks and footprints left by breeding females. An aluminium probe, 3 cm wide, 0.2 cm wide and 1 m long, was gently introduced into the sand to detect the eggs. Once located, the sand was removed until the first eggs appeared, and the depth between the first eggs and the surface was measured. Each egg was marked with a pencil on the upper surface to maintain the original egg position during incubation. For transport, eggs were placed in plastic coolers and covered with sand from the nest. Once emptied, the depth, length and width of the nests were measured. In 2003 all the eggs found were collected, whereas in subsequent years 30% of the eggs found were not removed so that egg-predation, maternal care and wild hatching success could be studied (Antelo, 2008). After transport, eggs were measured with callipers (± 0.1 mm) and weighted using a Pesola balance (± 5 g). Nesting date and egg viability were estimated based on the presence of the opaque band and its development (Ferguson, 1985; Antelo, 2008).

Egg incubation took place at the biological station, in a 6 m² room in which an 83-cm-high divider, 72 cm from the wall, formed compartments. Eggs were buried in sand at a depth of 30–50 cm and at temperatures between 28.7 and 33.3 °C, covered with the original nest sand. Each clutch was incubated with a 250 W infrared light. In the centre of the clutch a probe was positioned with an aluminium

sleeve (IP 65 Testo ± 0.2 °C) connected to an electronic thermometer (Datalogger Testo 175-T2, ± 0.1 °C). The sand was moistened 3–4 times a week, and air humidity was around 100%. Immediately after hatching, crocodiles were measured and weighed.

For wild nests, the size of nesting females was calculated from the nest depth, using 19 records presented by Colvée (1999) from captive *C. intermedius* breeding females. Mean temperature, thermal fluctuations and temperature variation with depth were recorded in wild nests. The same probes as described above were placed in the centre of the clutch and connected four times a day to an electronic thermometer (Datalogger Testo 175-T2, ± 0.1 °C). In total, 232 temperature measurements were recorded in eight different nests with depths from 24 to 44 cm. Temperature data were collected on three days per month during the incubation period (February, March and April 2006) at 6 h intervals (0300, 0900, 1500 and 2100). If a nest was predated during this period it was removed from the data collection and replaced by another nest. In order to quantify the expected temperature variation with depth, a 24 h test was carried out. Six sensors (IP 65 Testo ± 0.2 °C) were buried in a nest at different depths (10, 20, 30, 40, 50 and 60 cm), and temperatures were recorded every hour with an electronic thermometer (Datalogger Testo 175-T2, ± 0.1 °C).

RESULTS AND DISCUSSION

Reproductive chronology

Courtship and mating coincide with the end of the rainy season, while nesting and most of the incubation period occur during the dry season. Hatching takes place at the beginning of the following rainy season (Fig. 1).

Based on opaque band development, the nesting date of 44 clutches could be determined. No statistical differ-

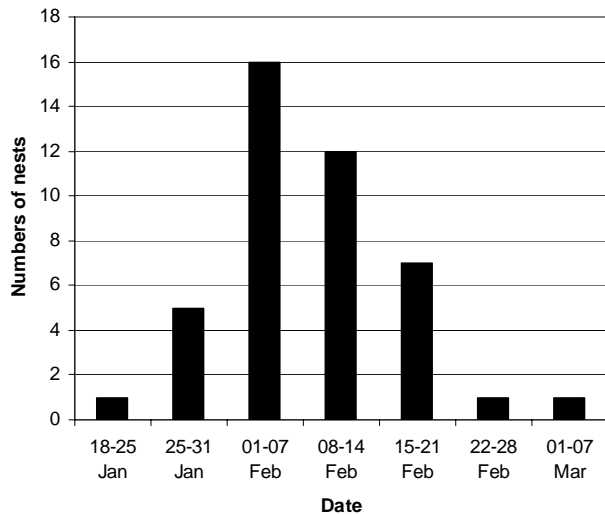


Fig. 2. *C. intermedius* nesting dates between 2003 and 2007.

ence in the nesting date occurred across the five study years ($P > 0.05$). The earliest clutch was found on 23 January, and the latest on 5 March. Nesting peaked in the first week of February (16 nests, 36% of the total), followed by the second week of February (12 nests, 27% of the total, Fig. 2).

We have only one record of incubation time in the wild, lasting 81 days. The mean incubation time for 35 clutches before they hatched in captivity was 90 days ($SD = 6.1$), with a minimum of 75 days (incubated at 33.0 °C) and a maximum of 103 days (incubated at 29.7 °C).

The dates of hatching of six wild nests ranged from 16 April to 15 May. The hatching of artificially incubated nests peaked during the first week of May (51%, 18 out of 35 clutches). The first and last hatchings occurred on 19 April and 29 May, respectively (Fig. 3).

As already noted by Gumilla (1745) in Orinoco river populations, *C. intermedius* reproduction starts in October with male territoriality and courtship displays. The nesting process is adapted to the water regime, and breeding females dig their nests in the dry season to minimize the risk of nest flooding. Hatching takes place with the onset of the rainy season, coinciding with an increase in insects and amphibian larvae. This seasonal pattern overlaps to the nearest month with other Orinoco crocodile populations, both wild (Medem, 1981; Ayarzagüena, 1987; Thorbjarnarson & Hernández, 1993a; Seijas & Chávez, 2002; Ardila-Robayo et al., 2002; Jiménez-Oraá et al., 2008) and captive (Ramo et al., 1992; Thorbjarnarson & Hernández, 1993a; Seijas, 1994; Lugo, 1995; Colvé, 1999).

In other hole-nesting species, egg-laying also takes place during the annual dry season (*Crocodylus niloticus*: Cott, 1961; *C. palustris*: Whitaker & Whitaker, 1984; *C. johnsoni*: Webb et al., 1983a). *Crocodylus acutus* has a nesting date that varies across its large range (Thorbjarnarson, 1988; Platt & Thorbjarnarson, 2000; Soberón et al., 2002; Casas-Andreu, 2003; Pérez & Escobedo-Galván, 2005). In Florida the incubation period

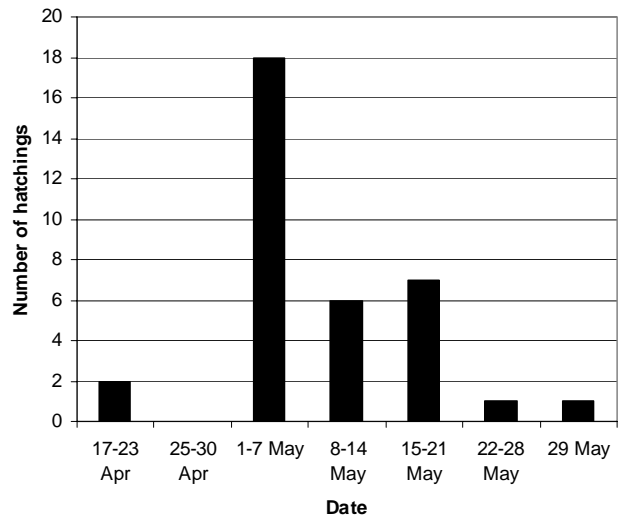


Fig. 3. Hatching chronology of artificially incubated nests.

of *C. acutus* mostly coincides with the rainy season, but sand mound-nests are still built (Kushlan & Mazzoti, 1989); nesting dates are probably defined more by temperature than rainfall (Thorbjarnarson, pers. comm.).

Artificial beaches, nest density and nest, clutch and egg characteristics

Between 2003 and 2007, at least 69 females nested in the artificial beaches (Fig. 4). The highest density (3.8 nests/km) was recorded for 2006, when 19 nests in 10 artificial beaches located within 5 km of the Caño Macanillal and the La Ramera Lagoon were found.

Nests holes are elliptic or almost round. Main parameters of nests, clutches and eggs are summarized in Table 1. The distance of the nests to the shore varied between 1 m and 25 m. Data for clutch size, mass, egg viability and egg dimensions are summarized in Table 2. No significant

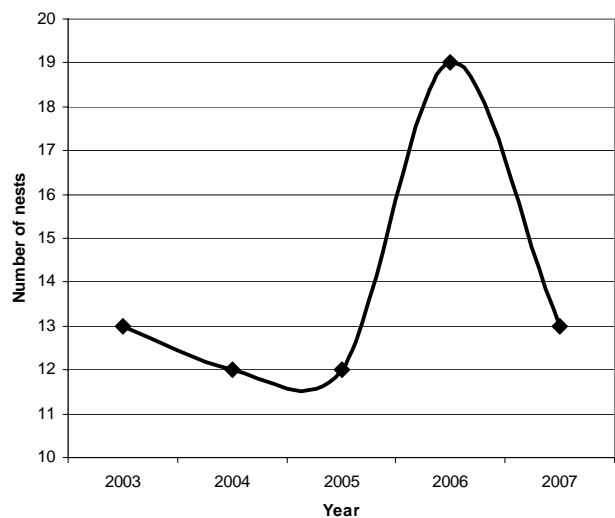


Fig. 4. Nests found between 2003 and 2007.

Table 1. Characteristics of nest and clutch attributes of *C. intermedius* (2003–2007).

Parameter	Mean \pm SD	Range	<i>n</i>
Nest characteristics			
Depth to top of clutch (cm)	26.35 \pm 7.9	12–47	31
Depth to bottom of clutch (cm)	42.63 \pm 9.7	24–70	34
Major axis of hole	35.04 \pm 6.3	25–46	21
Minor axis of hole	30.33 \pm 4.8	20–42	21
Clutch attributes			
Clutch size	41.2 \pm 9.6	20–59	43
Clutch mass (kg)	4.52 \pm 1.2	2.1–6.9	38
Egg length (cm)	7.61 \pm 0.3	6.6–8.5	691
Egg width (cm)	4.73 \pm 0.2	4.0–7.9	691
Egg mass (g)	111.07 \pm 8.71	85–133	691
Egg viability (%)	75.4 \pm 18.2	16.7–100	43

differences between years were found in any trait ($P > 0.05$).

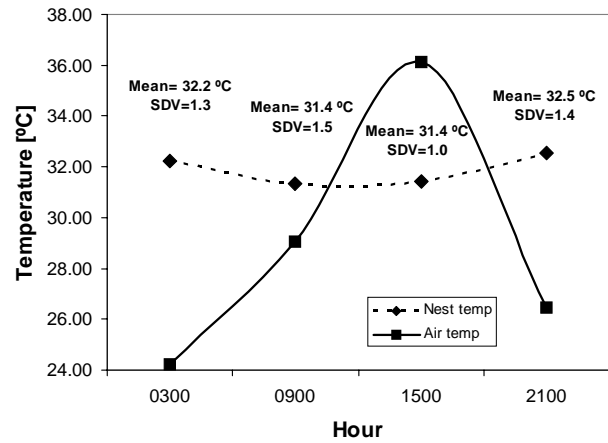
The Caño Macanillal–La Ramera lagoon system is one of the most important breeding areas for *C. intermedius*. The nest density observed in this study is among the highest reported for this species. In the Cojedes river system, nest density ranged from 5.27 to 0.38 nests/km (González-Fernández, 1995; Seijas & Chávez, 2002; Ávila-Manjón, 2008) and from 0.24 to 0.36 nests/km in the Capanaparo river range (Thorbjarnarson & Hernández, 1993a). However, nest density in the present study is largely determined by the artificial sand mounds.

Clutch and egg characteristics (Table 3) conform to those reported for other captive and wild *C. intermedius* populations. In our captive population, egg viability (75.4%) is lower than in the Capanaparo River (94.4%) (Thorbjarnarson & Hernández, 1993a), and lower than reported for other wild populations of crocodylians (*C. johnsoni*: 96–98%, Webb et al., 1983a; *C. acutus* in Haiti: 91.1%, Thorbjarnarson, 1988; *C. niloticus* in South Africa: 83%, Botha, 2005).

Females at the station are younger and presumably shorter than in the Capanaparo River (Antelo, 2008), which could be the reason for low egg viability, as pointed out for *C. johnsoni* (Webb et al., 1983a) and *A. mississippiensis* (Ferguson, 1985). On the other hand there is no correlation between the size of the *C. intermedius* breeding females and the percentage of fertilized eggs in either this study or in Agropecuaria Puerto Miranda (Colvée, 1999).

Table 2. Clutch and egg characteristics (2003–2007).

Year	Clutch size	Clutch mass	% fertility	<i>n</i>	Egg length	Egg width	Egg mass	<i>n</i>
2003	41.63	4433.3	80.8	9	7.61	4.73	110.01	297
2004	38.78	4329.3	78.3	9	7.67	4.73	111.33	143
2005	42.29	4477.7	74	7	7.57	4.71	108.92	74
2006	41.38	4699.3	65.5	13	7.59	4.74	113.57	177
2007	45.2	–	–	5	–	–	–	–

**Fig. 5.** Average nests and environmental temperatures over 24 hours. Data encompassing eight nests and 232 measurements over the incubation period (February–April) are presented.

Relationship between nest depth and breeding female size

Orinoco crocodile females mainly use their hind legs for nest digging (Thorbjarnarson & Hernández 1993b; Colvée 1999; Sigler 2007). As larger females have longer legs, it can be argued that larger females dig deeper nests. A linear regression based on 19 datapoints published in Colvée (1999) on nest depth and *C. intermedius* female total length in Agropecuaria Puerto Miranda, Guarico state revealed a regression with the equation $y = 3.14x + 152.48$ ($r = 0.82$; $P < 0.0001$), with an average error of 3% and a maximal error of 6.7%. Applying this formula to the nest depth measured in the present study, female total length ranged between 228 and 372 cm (mean 285 cm; $n = 34$). Thorbjarnarson & Hernández (1993a) point out that 250 cm is the minimum reproductive size for this species and the largest female measured (363 cm) was a wild individual (Antelo, 2008).

Wild nest temperatures

We took 232 measurements in eight nests. Average temperature was 31.9°C (SD=1.4), with a maximum of 35.6°C and a minimum of 27.3°C. Median thermal amplitude in the incubation cameras was 1.18°C, whereas it was 11.9°C in the surrounding environment (Fig. 5). The highest and lowest temperatures in the nest were measured at 2100 and 0900, respectively.

Figures 6 and 7 show the relationship between nest depth and nest temperature, and the correlation between nest depth and thermal amplitude. The thermal amplitude

Table 3. Clutch and eggs attributes in wild and captive *C. intermedius* populations. (-) No data. EBTRF: Estación de Biología Tropical Roberto Franco (Colombia). UNELLEZ: Universidad Nacional Experimental de los Llanos Occidentales “Ezequiel Zamora”.

	Clutch size	Clutch mass (g)	Egg mass (g)	Egg length (cm)	Egg width (cm)	Egg viability (%)	Source
Wild populations							
Capanaparo river	38.6	4490	115.9	–	–	94.4	Thorbjarnarson & Hernández, 1993a
Manapire river	43.9	–	–	7.9	4.8	–	Jiménez-Oraá et al., 2008
EFBS	41.2	4526	111.1	7.61	4.7	75.4	This study
Captive populations							
Masaguaral	30.7	3201	100.5	–	–	50.1	Thorbjarnarson & Hernández, 1993a
EBTRF	31.8	3044	112.7	7.82	4.8	76.8	Lugo (1995); Ramírez-Perilla & Urbano, 2002
UNELLEZ	42.5	–	107.3	7.6	4.7	93	Ramo et al., 1992; Seijas, 1994
Pto Miranda	39.4	3862.2	94.6	7.2	4.7	23.6	Colvée, 1999

decreases with depth ($r=0.98$; $P<0.0001$), and temperature remains almost constant when the nest is deeper than 40 cm. At a depth of 10 cm, the thermal amplitude is 7.4 °C and temperatures can reach above 35 °C, which is lethal for embryos of other crocodylian species (Lang & Andrews, 1994). At a depth of 20 cm, temperatures are sufficiently stable to allow the successful incubation of eggs, and at 30 cm thermal amplitude is minimal (1.3 °C). A depth of 30 cm corresponds with a size of 247 cm, when *C. intermedius* females become mature (Thorbjarnarson & Hernández 1993a; Antelo, 2008).

Hatching of artificially incubated eggs

As a part of the head-starting and reintroduction programme, 1085 eggs were collected from wild nests and incubated during the years 2003 to 2006.

Without taking into account the nonviable eggs (267; 24.6%), the hatching rate was 84.35% (Table 4). The incubation techniques used produced egg hatching rates that are comparable with other programmes (*C. niloticus* in Zimbabwe: 80–95%, Hutton & Jaarsveldt, 1987; *A. mississippiensis* in Louisiana: 91%, Joanen & McNease, 1987; *C. palustris* in India: 39%, Whitaker, 1987).

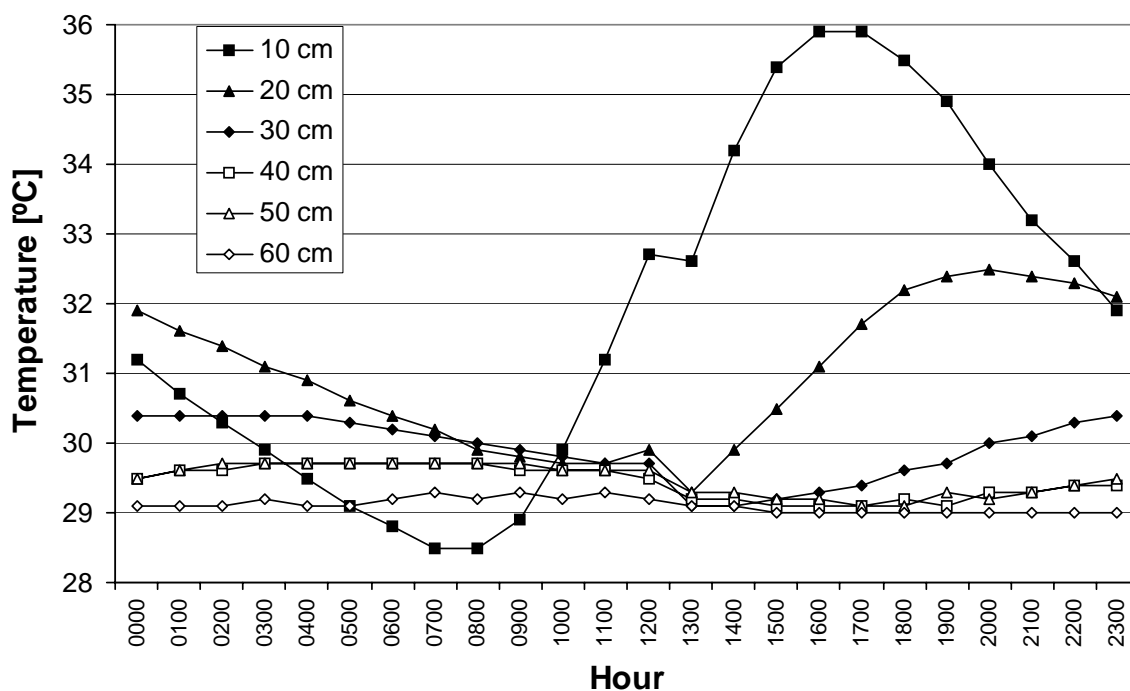


Fig. 6. Variation of air temperature and at intervals of 10 cm in depth measured at one nest. Temperatures were recorded on 14 April 2008.

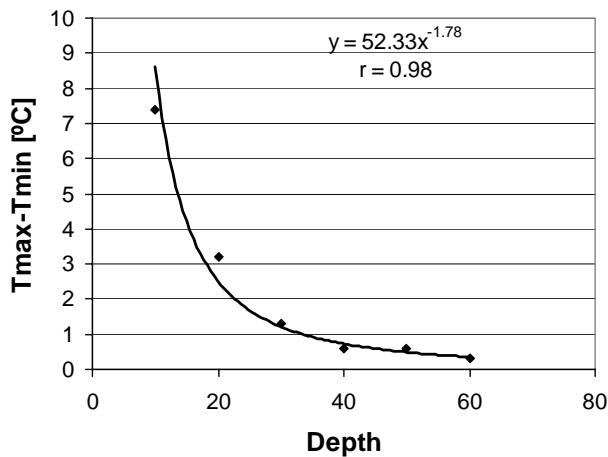


Fig. 7. Correlation between depth (cm) and thermal amplitude in a nest.

Mean total length and mass at hatching were 28.6 ± 1.37 cm (range 33.2–25 cm) and 66.9 ± 8.8 g (range 48–87.5 g), respectively, corresponding with values reported in other *C. intermedius* breeding centres (Puerto Miranda: 27.6 cm/70 g, Colvée, 1999; Estación de Biología Tropical Roberto Franco: 28 cm/77.4 g, Ramírez-Perilla & Urbano, 2002; Universidad Nacional Experimental de los Llanos Ezequiel Zamora: 28.5 cm/69.7 g, Ramo et al., 1992).

CONCLUSIONS

In the family Crocodylidae, hole-nesting only occurs during the dry season. As suggested by Cott (1961) for *C. niloticus*, this enables the emergence of suitable nesting places, lowers the probability of nest-flooding and facilitates hatching of crocodiles during the rainy season. Nest depth appears to be very suitable for estimating the total length of the corresponding breeding female. It is easy to measure in the field, and could also be used to calculate body length in other hole-nesting species. It is widely known that constant temperatures are maintained in the nests of crocodiles, but the relationship between thermal amplitude and the depth of the egg chamber had so far been unstudied. Our results suggest that *C. intermedius* females reach sexual maturity when they are large enough to excavate nests that are deep enough to ensure the successful development of their eggs.

Artificial beaches are an effective way to provide suitable habitats for nesting in the wild. This method also

Table 4. Viability of incubated *C. intermedius* eggs (2003–2006). *Twin crocodiles hatched from one egg.

	Year				Total
	2003	2004	2005	2006	
Incubated	296	247	208	334	1085
Nonviable	54	55	55	103	267
Failed	33	35	17	44	129
Hatched	209	157	136	188*	690

facilitates the collection of eggs because it limits the space available for nesting. A modification of this technique is successfully used in Bahía Cispatá (Colombia), where wild *C. acutus* females build their nests with supplied materials (Ulloa & Sierra, 2006). Observed nest dimensions are no different from nests excavated in natural beaches (Medem, 1981; Thorbjarnarson & Hernández, 1993a). Temperatures inside the nests are high and constant, and correspond to the viable incubation temperatures described for other crocodylians (Ferguson & Joanen, 1982; Webb et al., 1983b; Hutton, 1987; Lang et al., 1989; Lang & Andrews, 1994). Clutches that are not harvested or predated hatch normally.

The Orinoco crocodile conservation programme developed by us accelerates the growth of the Orinoco crocodile population in the area, reducing predation of eggs and hatchlings (Antelo, 2008). Captive breeding, head-starting and release have been defined by several authors as “halfway technology” in turtle conservation (Frazer, 1992; Seigel & Dodd, 2000; Moll & Moll, 2004). In our case, where habitat restoration was not necessary and illegal hunting was controlled through private security, these strategies have proved to be effective conservation tools. An excellent indicator of the success of the programme is that the number of breeding females is increasing.

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