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# Reproductive Ecology and Hatchling Growth Rates of the American Crocodile (*Crocodylus acutus*) on Coiba Island, Panama

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**Abstract.** We assessed the reproductive ecology of the American crocodile (*Crocodylus acutus*) on Coiba Island, Panama from January–December 2013. We examined nest site characteristics from January–April and hatchling survivorship from April–December. Ten nests were examined at three nesting localities where 30% of the nests were found under forest canopies and 70% were exposed to sunlight (distance to nearest tree =  $280 \pm 110$  cm). Half of the nests were built closer to the sea and the other half closer to bodies of freshwater ( $700 \pm 360$  cm). The nest dimensions were  $17.5 \pm 7.8$  cm from the top of the clutch to the surface,  $42.9 \pm 9.9$  cm from the bottom of the clutch to the surface, and  $35.9 \pm 3.6$  cm wide at the top of the nest cavity. The average soil conditions in the nests consistently had high concentrations of potassium (69.3 mg/L) and manganese (9.2 mg/L), moderate concentrations of phosphorus (6.6 mg/L) and iron (3.7 mg/L), and low concentrations of zinc (0.5 mg/L) and copper (0.0 mg/L). Cation exchange capacity showed consistently high concentrations of calcium (2.2 cmol/kg), moderate of magnesium (1.1 cmol/kg), and low in aluminum (0.1 cmol/kg). Volumetric water content was about  $25.0 \pm 2.6\%$  at the bottom and  $22.8 \pm .3\%$  in the middle of the clutches. Hatching success was 88.9%, of which 68.3% hatched by themselves or with the mother's aid and 20.6% hatched with our aid. Mean size of the mother was  $219 \pm 6.2$  cm total length (TL) and  $115.9 \pm 3.0$  cm snout–vent length (SVL). The incubation period was estimated to be 85–88 days. TL and SVL growth rate of those individuals were 0.03–0.16 cm/day and 0.00–0.09 cm/day, respectively. Population size was estimated to be 218.6 hatchlings in 22.4 km<sup>2</sup>; the hatchling population declined 65.7% after the first 2 months (May and June) and 95.9% by July, leaving only 0.5% remaining by December. This is the first study to assess nest-site characteristics and estimate hatchling survival in a Pacific population of American crocodiles.

**Keywords.** Conservation; Habitat; Hatching success; Nest-site selection; Parental care.

**Resumen.** Se evaluó la ecología reproductiva de *Crocodylus acutus* en la Isla de Coiba, Panamá entre enero y diciembre del 2013. Se examinaron los sitios de anidación entre enero y abril y la supervivencia de los neonatos entre abril y diciembre. Diez nidos fueron examinados en tres sectores, de los cuales 30% se encontraron bajo cobertura forestal y 70% expuestos (distancia al árbol más cercano  $280 \pm 110$  m). La mitad de los nidos se encontraron cerca al mar y la otra mitad cerca de cuerpos de agua dulce ( $700 \pm 360$  cm). Las dimensiones de los nidos fueron  $17.5 \pm 7.8$  cm desde la parte superior de la cámara hasta la superficie,  $42.9 \pm 9.9$  cm desde el fondo y  $35.9 \pm 3.6$  cm de ancho de cámara. Las condiciones promedio del suelo en los nidos fueron altas concentraciones de potasio (69.3 mg/L) y manganeso (9.2 mg/L), moderadas de fósforo (6.6 mg/L) y hierro (3.7 mg/L), y bajas de zinc (0.5 mg/L) y cobre (0.0 mg/L). La capacidad de intercambio catiónico mostró altas concentraciones de calcio (2.2 cmol/kg), moderadas de magnesio (1.1 cmol/kg) y bajas de aluminio (0.1 cmol/L). El contenido volumétrico de agua fue  $25.0 \pm 2.6\%$  en el fondo y  $22.8 \pm 5.3\%$  en el medio. El éxito de eclosión fue 88.9%, de los cuales el 68.3% eclosionaron por sí mismos o con la ayuda de la madre y el 20.6% con la ayuda de los investigadores. El promedio de tamaño de las hembras fue  $219 \pm 6.2$  cm longitud total (LT) y  $115.9 \pm 3.0$  cm longitud rostro-cloaca (LRC). El periodo de incubación se estimó entre 85 y 88 días. Las tasas de crecimiento en los neonatos oscilaron entre 0.03 y 0.16 cm/día LT y 0.00 y 0.09 cm/día LRC. El tamaño poblacional se estimó en 218.6 neonatos en 22.4 km<sup>2</sup>. Esta población declinó 65.7% después de los primeros dos meses (mayo y junio) y 95.9% después del tercero (julio), quedando solamente el 0.5% de la población estimada en diciembre. Este es el primer estudio que evalúa la anidación y estima la supervivencia de neonatos en una población de *C. acutus* en el Pacífico.

## INTRODUCTION

The American crocodile (*Crocodylus acutus* Cuvier, 1807) is widely distributed across the Neotropics along the Atlantic, Caribbean, and Pacific coasts, from Florida, USA to Venezuela and from Mexico to northern Peru (Thorbjarnarson, 2010). Despite their large distribution, populations of *C. acutus* are threatened because of past and current poaching and habitat destruction (Platt and Thorbjarnarson, 2000a). There are only a few islands with known populations of *C. acutus* on the Pacific side of the

species' distribution in Panama (Las Perlas Archipelago and Coiba, Gobernadora, and Leones Islands) and Mexico (Maria Magdalena Island; Casas-Andreu, 1992; Thorbjarnarson et al., 2006); until now none of these populations have been studied.

Currently, *Crocodylus acutus* is considered to be vulnerable (Ponce-Campos et al., 2012) by the International Union for Conservation of Nature and Natural Resources (IUCN) and listed on Appendix I of the Conservation on Trade in Endangered Species of Flora and Fauna (CITES, 2012). Although direct threats to the species are known,

our overall understanding of the different populations' ecology is too limited to develop and implement successful management plans across the species' range (Thorbjarnarson, 2010; Balaguera-Reina et al., 2014). Centrally situated in the range of *C. acutus* is Panama, where the species is considered endangered (Ibáñez, 2006) and our understanding of its ecology is poor (Venegas-Anaya et al., 2014).

As with most crocodylians, the reproductive ecology of *Crocodylus acutus* consists of five distinct stages including courtship, mating, nesting, brooding, and hatching. Some of these components are well studied in populations in Florida, USA (Mazzotti, 1983), Mexico (Alvarez del Toro, 1974), Haiti (Thorbjarnarson, 1989), and Colombia (Medem, 1981). However, in most countries we have little or no knowledge about these reproductive stages and whether they vary across different portions of the species range. Additionally, there is hardly any information on growth rates and hatchling survivorship in any population of the species (Thorbjarnarson, 1988; Platt and Thorbjarnarson, 2000b), even though there is a fair understanding about these traits in many other crocodylians. For example, from research on other species we know that age, sex, genetics, incubation conditions, and other biotic characteristics of the environment play important roles in determining growth rates and survivorship, confirming that crocodylian reproduction is a complex process affected by multiple of factors (Webb et al., 1983; Da Silveira et al., 2013).

Coiba National Park (CNP) is located in the Gulf of Chiriqui on the Pacific side of the Republic of Panama. Currently, it is the largest marine preserve along the entire Pacific coast of Central America and consists of the large island of Coiba and 38 smaller islands (Maté et al., 2009). Coiba and the surrounding islands are land-bridge islands that separated from continental Panama ca. 12,000–18,000 years ago (Ibáñez, 2006). CNP is included in the World Heritage List under natural criteria II and IV due to its biological and ecological importance (Maté et al., 2009). It is also part of the Tropical Eastern Pacific Marine Corridor, which is critical for the migration of many marine species (CMNUS, 2002).

It has been suggested that Coiba Island may harbor one of the largest remaining populations of *Crocodylus acutus* across Central America with approximately 500–1000 individuals (Thorbjarnarson, 2010), which further highlights the importance of *C. acutus* management in CNP. This population was seriously depleted in the past, mainly by unsustainable exploitation by locals, sport-hunters, ranchers, and fishermen (Powell, 1971). Even though the species is protected by national laws and hunting is strictly prohibited, additional information about the species' conservation status and its ecology will be critical for creating an effective conservation plan in Panama. The aim of our study was to assess the reproductive ecology and

early stage growth rates (hatchlings and juveniles) for the first time in a population of *C. acutus* in a southeastern bay of Coiba Island.

## MATERIALS AND METHODS

From January–April of 2013 we carried out daily transect surveys in the coastal zone from Boca Grande to Punta Felipa (10.3 km, corresponding to 5.2% of the total perimeter of Coiba Island) in a southeastern bay of Coiba Island to search for nests and female *Crocodylus acutus* (Fig. 1). The area encompassed five kinds of local ecosystems: beaches, dry forest, riparian forest, mangrove, and rocky coastline.

Nesting areas were identified by the presence of excavated nests, eggshells, fresh tracks, and/or other visible crocodile-mediated disturbances in the sand. These areas were carefully excavated to expose clutches. Prior to excavation, external features of the nest were recorded (length and width of disturbed area, and level of canopy cover) as well as the distance to the nearest body of water, tree, and other crocodile nests. All nests were excavated to determine clutch size and egg viability and measure the depth and width of the clutch. Egg viability was determined by the presence of an opaque band on the center of the uppermost surface of fertile egg, and oviposition dating was estimated based on the width of the band (Ferguson, 1985). All eggs were measured and weighed with analog calipers ( $\pm 0.1$  mm) and spring scales ( $\pm 1$  g), respectively, and marked using a pencil on the uppermost surface with a small cross to avoid changes in egg polarity when eggs were returned to the nest. After females abandoned their clutches, we waited 1–2 hours and resumed nest excavation to help any remaining eggs hatch, breaking the egg shell and thus facilitating the release of the hatchling. At the same time, we determined the numbers of unhatched eggs, nonviable eggs, dead hatchlings, and eggs that hatched with the aid of the mother or our team, providing us novel insights into the exact initial moments of clutch hatching and maternal behaviors that might affect the survivability of hatchlings.

Whenever possible, females were captured and measured. Total length (TL) and snout–vent length (SVL: tip of snout to anterior margin of cloaca; Webb and Messel, 1978) measurements were taken, and each crocodile was marked by notching the dorsal scutes in a systematic marking series on the tail (Jennings et al., 1991). If capture was not possible, length was estimated from the rear-foot tracks found at the nest site (Platt and Thorbjarnarson, 2000b). Camera traps were placed at the nests to record maternal behaviors and the timing of hatching.

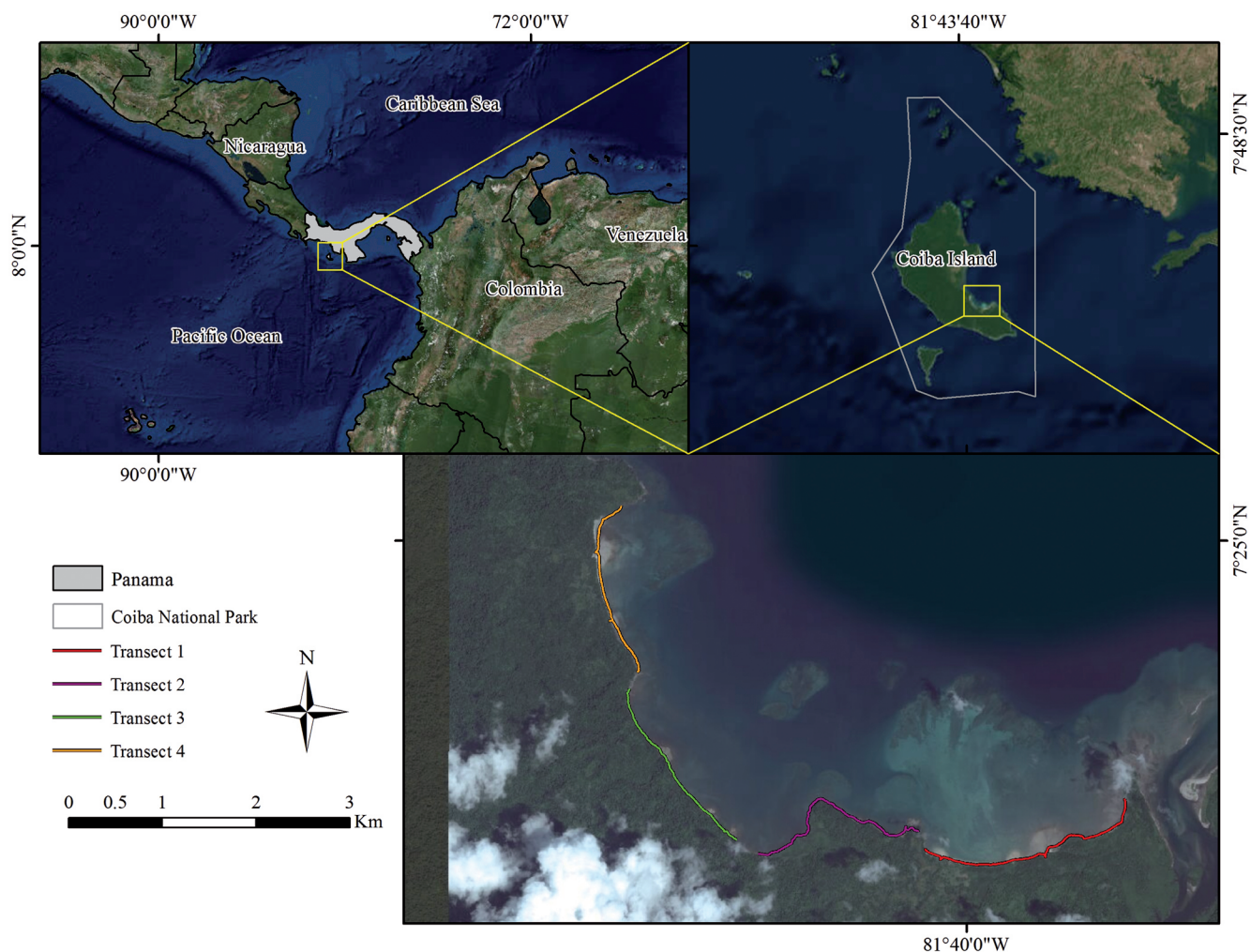
Moisture sensors (Vegetronix®) were placed in the bottom and middle of the clutches (delay time 30 min) to determine the volumetric water content (VWC) within

the nest. Vegetation cover at the nesting and nursery areas (places where hatchlings spend the first months, commonly close the nesting areas) was assessed using three 100 × 100 m plots, which included all the nests found to determine the amount of canopy cover (area of shading), tree height, diameter at breast height (DBH), vegetation richness, and tree density. Simpson dominance, Margalef richness, and Shannon diversity indices were calculated for the vegetation cover data. We also used ArcGIS 10.1 (ESRI, 2012) and the most current maps of the area (Maté et al., 2009) to describe the land cover. Soil samples were taken from the bottom of each clutch, packed, and transported to the Agriculture Research Institute of Panama (IDIAP) to determine the chemical and physical properties based on standard protocols.

For one week per month from April–December 2013 we carried out nightly transect surveys to search for hatchling juveniles across the coastal zone. Over this nine-month period, individuals were captured, measured (TL; SVL; tail length, TaL.; head length-, HL; head width-HW; mass), marked, and released at the site of capture.

During these transect surveys we also searched for adults (males and females) to record reproductive behaviors (ag- onistic behavior, courtship, or mating).

Individual growth rate was estimated by calculating the geometric mean difference in TL and SVL between capture-recapture events (Campos et al., 2013). Population size and mark-recapture models were estimated using Mark software (White and Burnham, 1999). We used live recapture (i.e., Cormack-Jolly-Seber models based on survival,  $\phi$ , and recapture,  $p$ , probabilities) and Papan formulation (i.e., Jolly-Seber models using  $\phi$  and  $p$  as well as probability of entry,  $pent$ , and initial population size,  $N$ ; see White and Burnham, 1999) to determine the best model to describe our population and also to estimate the hatchling population size. We estimated the activity patterns of hatchlings and their movements based on geo-referenced points collected using a GPS (Global Positioning System) device and analyzed using ArcGIS 10.1 (ESRI, 2012). The size of the study area was estimated based on the extent of the coastline from Boca Grande to Punta Felipa and calculating a 1 km buffer around it.



**Figure 1.** Study area and transects assessed from Boca Grande to Punta Felipa in Coiba National Park.

The growth rate and morphometric analyses were conducted using InfoStat and R statistical software packages (Di Rienzo et al., 2013; R Development Core Team, 2012). Significance of changes in variables was estimated from one-sample *t*-tests and nonparametric analysis of variance (Kruskal-Wallis due to sample size; Di Rienzo et al., 2013). We report the accuracy of sample means using a standard deviation of  $\pm 0.1$  (SD) and the accuracy of population models as standard error of  $\pm 0.1$  (SE by default calculation in Mark software).

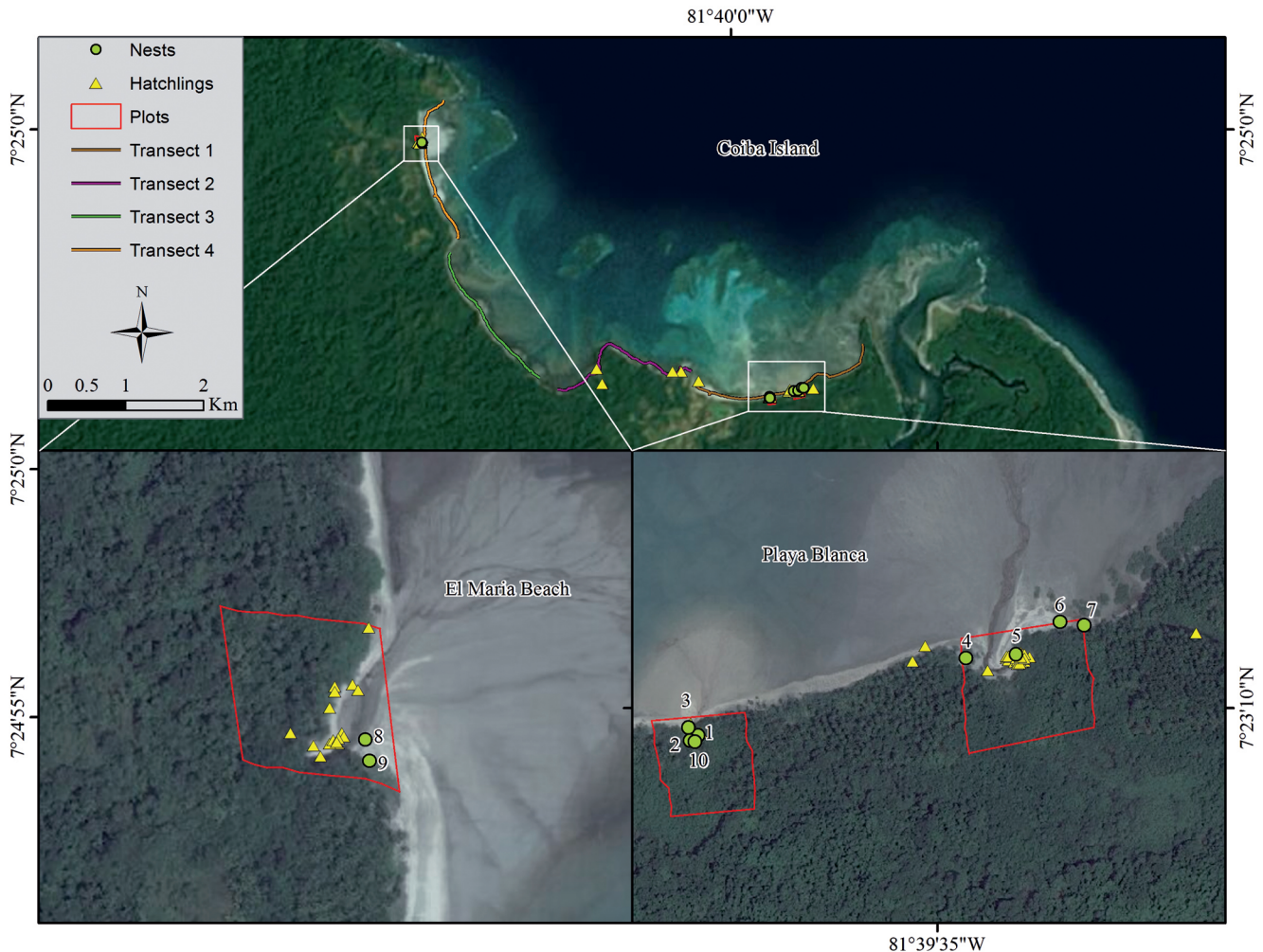
## RESULTS

Three nesting areas and 10 individual nests were identified from Punta Felipa to Boca Grande in the southeastern part of Coiba Island (Fig. 2). Most nest areas were located on Playa Blanca, with eight clutches in total (Fig. 2, Table 1). Thirty percent of the nests were found under forest canopies and 70% were exposed to sunlight

(distance to the nearest tree  $\bar{X} = 280 \pm 110$  cm). One clutch (nest 1) was found in a mangrove forest (*Conocarpus erectus* Linnaeus, 1753) with minimal exposure to sunlight, two clutches (nests 5 and 6) were within dry forest (under *Prosopis juliflora* (Swartz), DC trees), and the other nests were found on the beach without canopy cover (Fig. 2).

We found a colonial nesting area (places with more than one nest in a reduced area, determined by the distance among each other; see Platt and Thorbjarnarson, 2000b) on Playa Blanca (clutches 1, 2, and 10; distance between nests  $\bar{X} = 620 \pm 130$  cm). Nine of the 10 nests were built as vertical shafts into the soil and one was a sloping cavity into a sandbank ( $\sim 60^\circ$  slope). Fifty percent were nearer to the sea than to freshwater ( $> 1,500$  cm) and 50% were closer to bodies of freshwater, at an average distance of  $700 \pm 360$  cm (Table 2).

The average nest was  $17.5 \pm 7.8$  cm from the top of the egg clutch to the surface and  $42.9 \pm 9.9$  cm from the bottom of the clutch to the surface, with a width of  $35.9 \pm 3.6$  cm. We could determine in five nests the clutch



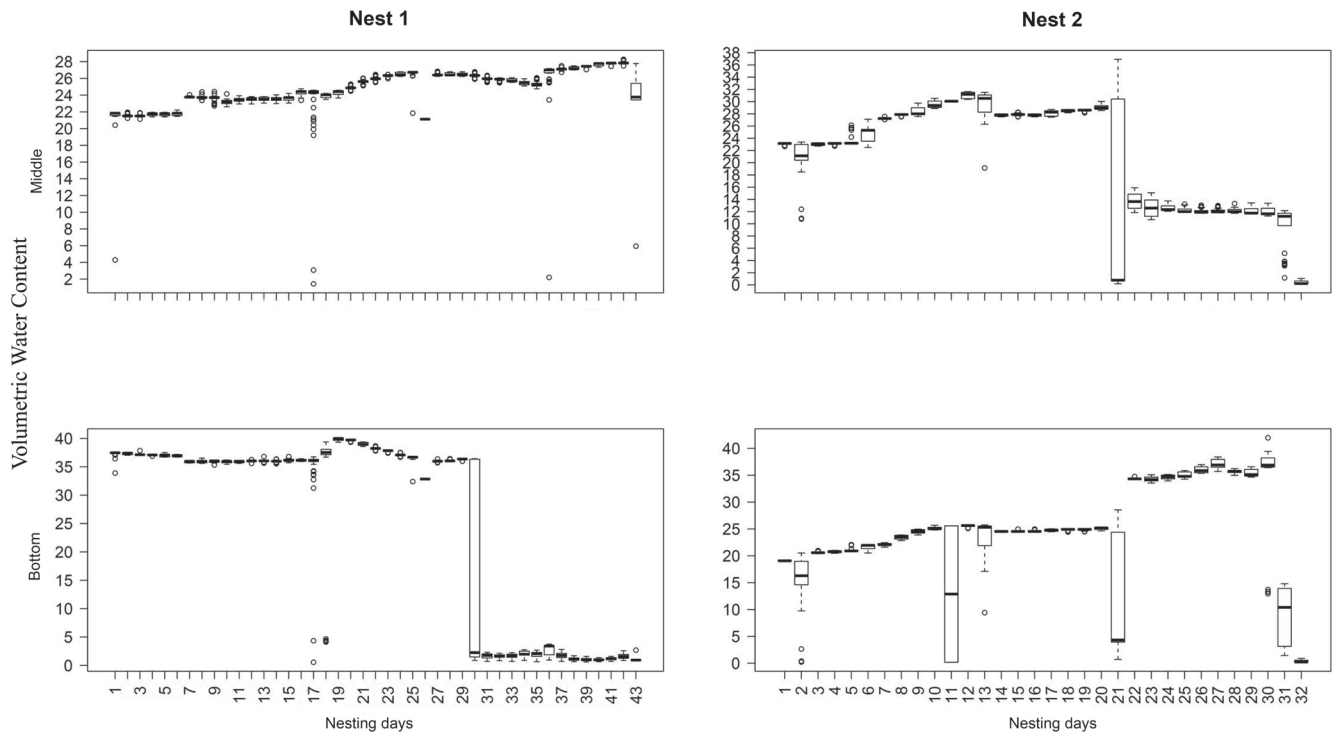
**Figure 2.** Nests found and hatchling distribution from Boca Grande to Punta Felipa in Coiba National Park. Red squares are the  $100 \times 100$  m plots assessed to determine the vegetation cover in the nesting and nursery areas. Light green spots are the nests found and yellow triangles are the hatchling-juveniles geo-references obtained across the study.

**Table 1.** Information for each nest (NID) on hatching date (H. Date), sector, total number of eggs (T.E.), number of eggshells (E.S.), nonviable eggs (N.E.), unhatched eggs (U.H.E.), dead hatchlings (D.H.), hatched with mother's help (H.M.H.), and hatched without mother help (H.W.H.) on Playa Baluca (P.B.) and El Maria beach (E.M.) on Coiba Island 2013.

NID	H. Date	Sector	T.E.	E.S.	N.E.	U.H.E.	D.H.	H.M.H.	H.W.H.
1	16 Apr	P.B.	40		1	1	1	26	11
2	6 Apr	P.B.	28			1		27	0
3	9 Apr	P.B.	16		0	6		1	9
4	10 Apr	P.B.	N/I	7					
5	10 Apr	P.B.	24		0	1		17	6
6	11 Apr	P.B.	N/I	16					
7	11 Apr	P.B.	N/I	7					
8	14 Apr	E.M.	N/I	10					
9	13 Apr	E.M.	N/I	10					
10	15 Apr	P.B.	18		0	3		15	0
<b>X</b>			25.2	10.0	0.3	2.4		17.2	5.2
<b>SD</b>			9.5	3.7	0.5	2.2		10.5	5.1
<b>Max</b>			40	16	1	6		27.0	11.0
<b>Min</b>			16	7	0	1		1.0	0.0
<b>Total</b>			126		1	12		86	26

**Table 2.** Physical and biological attributes of American crocodile nests on Coiba Island.

Parameter	Mean ± 0.1 SD	Range	N
<b>Nest characteristic</b>			
Depth to top of clutch (cm)	17.5 ± 7.8	12–30	2
Depth to bottom of clutch (cm)	42.9 ± 9.9	31–60	10
Width of clutch (cm)	35.9 ± 3.6	29–40	10
Distance to water (cm)	700 ± 360	130–1,100	5
Distance to nearest tree (cm)	200 ± 160	0–480	10
Distance to nearest nest (cm)	22.5 ± 19.1	5.5–55.8	10
Volumetric water content (%) nest 1 middle	25 ± 2.2	1.4–28.3	1787
Volumetric water content (%) nest 1 Bottom	24.6 ± 16.8	0.6–40.1	1787
Volumetric water content (%) nest 2 middle	20.6 ± 8.6	0.2–36.9	1263
Volumetric water content (%) nest 2 Bottom	25.5 ± 8.7	0.2–42.0	1263
<b>Clutch attributes</b>			
Clutch size	25.2 ± 9.5	16–40	5
Egg length (cm)	7.4 ± 0.4	6.3–8.4	89
Egg width (cm)	4.0 ± 0.7	3.0–5.0	52
Proportion	0.5 ± 0.1	0.4–0.7	52
Egg mass (g)	97.1 ± 4.3	83.0–108.0	68
Eggs hatched with mother help (%)	68.3	0–100	126
Eggs hatched with our help (%)	20.6	0–100	126
Nonviable eggs (%)	0.8	0–100	126
Non-hatched eggs (%)	9.5	0–100	126
Hatchling dead at nest (%)	0.8	0–100	126
Hatched success (%)	88.9	0–100	126
<b>Mother attributes</b>			
Total length (cm)	219 ± 6.2	208–226	5
Body length (cm)	115.9 ± 0.0	111.5–118	4
Mass (kg)	35.9 ± 4.0	32–41.5	4
<b>Parental care</b>			
Lapse among visits nest 1 (days)	18.7 ± 18	1–88	4
Lapse among visits nest 2 (days)	35 ± 48.1	1–85	2



**Figure 3.** Volumetric water content box-plot for nests 1 and 2, recording the values in the middle and bottom part of each nest throughout the entire nesting period.

size (average =  $25.2 \pm 9.5$  eggs; total eggs = 126) due to they were found before, during, or immediately after hatching, allowing us to count the total number of eggs and hatchlings. Average egg dimensions were  $7.4 \pm 0.4$  cm in length,  $4.0 \pm 0.7$  cm in width, and  $97.1 \pm 4.3$  g in mass (Table 2). Volumetric water content (VWC) was only measured in nests 1 and 2 as they were found very shortly after oviposition (other nests were discovered later in the incubation period and could not be monitored through the entire duration of the study). The mean VWC of nest 1 was  $25.4 \pm 16.3\%$  at the bottom of the clutch and  $24.7 \pm 0.1\%$  at the middle of the clutch, whereas for nest 2 it was  $24.6 \pm 0.8\%$  at the bottom and  $20.9 \pm 0.5\%$  at the middle (Fig. 3). Overall, VWC in nests was about  $25.0 \pm 12.6\%$  at the bottom and  $22.8 \pm 5.3\%$  in the middle of the clutches.

Soil had high mean concentrations of potassium (69.3 mg/L) and manganese (9.2 mg/L), moderate mean concentrations of phosphorus (6.6 mg/L) and Iron (3.7 mg/L), and low mean concentrations of zinc (0.5 mg/L) and copper (0.0 mg/L); all values were consistent for all nests (Kruskal-Wallis test  $\geq 0.05$ ). Otherwise, cation exchange capacity showed high concentrations of calcium (2.2 cmol/kg), moderate of magnesium (1.1 cmol/kg) and low of aluminum (0.1 cmol/L), which was also consistent for all nests ( $n = 10$ ; Kruskal-Wallis test  $\geq 0.05$ ; Table 3).

Hatching success (total eggs hatched  $\times 100$  / total clutch size) for the incubation cycle was 88.9% (112

hatchlings), of which 68.3% (86 hatchlings) emerged by themselves or with the mother's help (natural hatching), and 20.6% (26 hatchlings) hatched with our assistance. Hatchling mean measurements were TL =  $27.8 \pm 0.8$  cm, SVL =  $13.6 \pm 0.5$  cm, TaL =  $14.3 \pm 0.7$  cm, HL =  $4.3 \pm 0.1$  cm, HW =  $2.2 \pm 0.1$  cm, and mass =  $69.7 \pm 7.3$  g ( $n = 90$ ).

We found that some females only helped to hatch superficial eggs, neglecting the lower eggs (nests 1, 3, and 5). The opaque bands, which is easy to see in daylight, were only examined in nests 1 and 2, which were found in early stages of incubation; width of the band was 41% and 55% of the average egg length, respectively. Based on Ferguson's (1985) suggestions, these values correspond to the eggs at nest 1 being laid 12 days prior to discovery and at nest 2 20 days prior to discovery. Based on our observations of hatching, the estimated incubation period was 88 days for nest 1 and 85 days for nest 2.

We captured four of the mothers (at nests 1, 2, 3, and 7) and found one rear-track at nest 9. The mean size of these animals was TL =  $219 \pm 0.2$  cm ( $n = 5$ ) and SVL =  $115.9 \pm 3.0$  cm ( $n = 4$ ). We only captured one adult male (TL = 199.5 cm) at the nesting area on 31 January, in close proximity to nests 4 and 5.

Nests 1 and 2 were monitored using camera traps to record parental behavior. After nest 1 was completed, the female was recorded four times on top of the nest (counting the day of hatching; Video S1) with a mean of  $18.7 \pm 18$  days between visits (first lapse between visits was 39 days, the second lapse was 5 days, and the third

**Table 3.** Soil chemical conditions of American crocodile nests on Coiba Island. N: Nest, % OM: Organic Matter.

N	% OM	pH	P mg/L	K mg/L	Ca Cmol/kg	Mg Cmol/kg	Al Cmol/kg	Mn mg/L	Fe mg/L	Zn mg/L	Cu mg/L
1	0	8.5	9	27.1	2.2	1.5	0.3	9.6	2.9	0.4	0
2	0	8.5	6	22.7	1.5	0.6	0.2	6.2	2.2	0.1	0
3	0	7.8	5	63.7	1.8	1.5	0.1	11.3	1.5	0.3	0
4	0.01	8	19	72.9	2.3	0.8	0.1	9.1	2.2	0.3	0
5	0	7.9	11	132.5	1.6	1.1	0.1	11.4	5.1	0.5	0.02
6	0	7.8	6	61.4	2.6	1	0.1	10.6	4.2	0.5	0
7	0	8.1	10	65.3	1.7	0.8	0.1	12	5.9	0.6	0
8	0	7.9	0	94.3	3.4	1.9	0.1	6.8	4.3	0.9	0
9	0	8.3	0	106.4	2.8	1.6	0.1	6.3	4.7	0.7	0
10	0	8.1	0	46.4	1.9	0.3	0.1	8.4	4.1	0.5	0.1
<b>X</b>			6.6	69.3	2.2	1.1	0.1	9.2	3.7	0.5	0.0
<b>SD</b>			6.0	34.3	0.6	0.5	0.1	2.2	1.4	0.2	0.0
<b>Max</b>			19	132.5	3.4	1.9	0.3	12	5.9	0.9	0.1
<b>Min</b>			0	22.7	1.5	0.3	0.1	6.2	1.5	0.1	0

lapse was 12 days). The majority of these visits were at night between 19:00–22:30 h and lasted no more than 5 min. However, on the day of hatching, the nest 1 female arrived at the nest at 01:35 h and started uncovering and assisting the young to exit the nest until 05:30 h, at which time she left the area. She returned at 22:00 h of the same day to finish that work until 02:30 h of the next day (total attendance time = 8 h 25 min). One interesting observation about this female is that when she came to uncover the nest the fourth time, her right forelimb showed evidence of recent mutilation. This must have happened within the two weeks leading up to that day, as she had been seen continuously for 2 months. The female who built nest 2 visited the nest three times (counting the day of hatching), always between 21:00–01:00 h. These nocturnal visits occurred during the first days of February (one day lapsed between the first and second visit) and the beginning of April (day of hatching, 69 days since the previous visit) between 21:30–01:30 h.

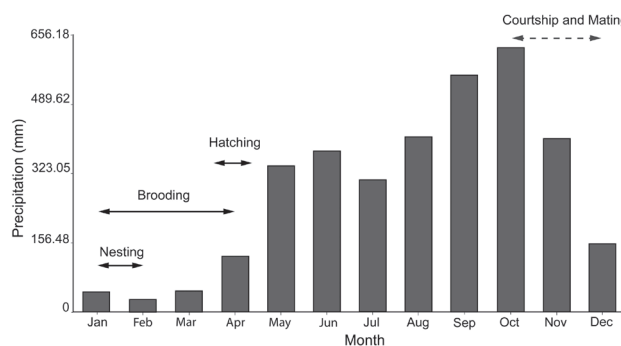
We observed three of the five reproductive events (nesting, brooding, and hatching; Fig. 4) commonly recognized in crocodiles (Antelo et al., 2010). Although we monitored the population year-round across the coastal areas (beaches, mangroves, riparian forest, dry forest, and rocky coastline), we never observed groups or pairs of males and females in courtship, mating, or performing agonistic behaviors.

In general, these three plots designed to characterize vegetative cover in reproductive areas in all cases showed characteristics of mangrove forests in regeneration dominated by *Laguncularia racemosa* (Linnaeus) Gaertner, 1807 (white mangrove). These were associated with other mangrove species (*Rhizophora mangle* Linnaeus, 1753; plot 2), tall grasses (*Gynerium sagittatum* (Aublet) Beauvois, 1812; plot 3) and flowering trees (*Talipariti tiliaceum* (Linnaeus) Fryxell, 2001; plot 1) in each of the plots. Plots 2 and 3 showed similarities among Simpson's index of dominance of plants (0.2 and 0.3, respectively), Margalef

richness (2.7 and 2.8, respectively), and Shannon diversity values (3.3 and 3.1, respectively). Plot 1 had higher dominance and lower diversity levels (Simpson index 0.7, Margalef richness index 2.5, and Shannon index 2.4) than plots 2 and 3. Canopy cover in the three plots had means of  $310 \pm 160$  cm,  $230 \pm 40$  cm, and  $250 \pm 150$  cm, respectively; otherwise, forest height and DBH were closely correlated among plots (forest height:  $580 \pm 300$  cm,  $590 \pm 50$  cm,  $560 \pm 310$  cm; DBH:  $43.8 \pm 27.6$  cm,  $44.1 \pm 32.4$ ,  $48.2 \pm 28.1$  cm, respectively).

Based on the current cartography of Coiba Island (Maté et al., 2009) the nesting localities (from Punta Felipa to Boca Grande approximately one km perpendicular to the coastal line) had seven categories of vegetation cover: rainforest (77.8%), secondary forest (9.3%), stubble (5.2%), paddock (3.5%), mangrove (2.9%), beach (0.6%), and beach vegetation (0.6%). All nests were found in or in close proximity to mangrove forest (dominated by *Laguncularia racemosa*), secondary forest (dominated by *Prosopis juliflora*) and beach (either bare or dominated by *Batis maritima* Linnaeus, 1759).

From April–December we carried out four nocturnal transects (averaging  $2.4 \pm 0.32$  km) per month to search for hatchlings across the coastal zone. We captured 112



**Figure 4.** Reproductive ecology throughout the year in relation to mean rainfall recorded on Coiba Island.



individuals that hatched in 2013 from April–December (88.9% of total eggs found) which covered two age states, hatchlings (< 30 cm TL, determined by presence of yolk sac and umbilical scar still open) and juveniles (30–90 cm TL, size when all yolk has been totally reabsorbed, yolk sac is dried, and the umbilical scar is completely closed; Thorbjarnarson, 1989; Platt and Thorbjarnarson, 2000a), the majority in April (90 hatchlings captured on nests after hatched day, corresponding to 80.4% of total hatchlings captured) with much fewer captures (22, new captures) in the following months. The capture rate was highest in April (80.4%) and May (13.4%) and decreased over subsequent months (from 2.7 to 0.9%). Of those, 83.9% were captured once, 13.4% twice, and 0.9% three, four, and five times, respectively. The individual mean measurements throughout the study were TL = 30.4 ± 5.0 cm, SVL = 15.0 ± 2.8 cm, TaL = 15.4 ± 2.3 cm, HL = 4.7 ± .9 cm, HW = 2.4 ± 0.3 cm, and mass = 80.0 ± 50.0 g ( $n = 112$ ). The individual mean measurements in the last month (maximum size recorded) were TL = 52.9 ± 3.6 cm, SVL = 27.3 ± 1.8 cm, TaL = 25.7 ± 1.9 cm, HL = 8.6 ± .8 cm, HW = 3.9.4 ± 0.0 cm, and mass = 350.0 ± 80.0 g ( $n = 2$ ). We did not find a statistically significant linear relationship among any of these variables (TL, SVL, and W =  $n$ : 142, linear regression  $P > 0.05$ ), nor the period of time evaluated (months). A nonlinear regression test determined that Gompertz's model (Gompertz, 1825) best described the growth through these two age states (hatchlings and juveniles) from April–December, with all terms of the model contributing significantly ( $P < 0.05$ ; Fig. 5). TL and SVL growth rates were 0.03–0.16 cm/day and 0.00–0.09 cm/day, respectively (Fig. 6).

In general, all hatchlings stayed close to the nest in both brackish and seawater. For the first 15 d after hatching, the average distance from the nest at which hatchlings were found was 1,600 ± 1,030 cm and increased to 17,490 ± 3,370 cm within a month of hatching. In May we found one hatchling 11,850 cm (in a mangrove forest) from its hatching site. During July, August, and September, hatchlings showed presumably low movement (0.005 ± 0.004 km, 0.015 ± 0.012 km, 0.029 ± 0.010 km, respectively). In October (6 months after hatching) we found one hatchling 2.9 km from the nest site (Fig. 2). Although we did not follow hatchling movements systematically, these long distances traveled must have been by sea as we did not identify any flowing water sources between the nest sites and these secondary observations and *Crocodylus acutus* hatchlings and early juveniles do not travel long distances overland (Thorbjarnarson, 1989).

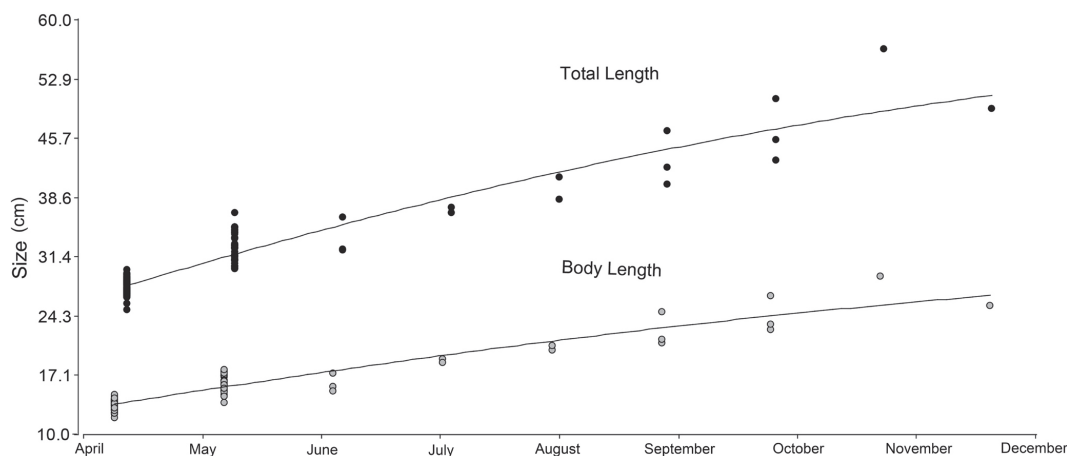
At nest 3, we observed a female carrying a hatchling from the nest directly to the sea, which has not been documented previously for *Crocodylus acutus*. One month after hatching during the rainy season, we began to see groups of hatchlings in the sea. Sometimes individuals were seen alone, most likely due to the action of waves and currents.

Even though we did not systematically record hatchling predation, we did observe the common black-hawk, *Buteogallus anthracinus* (Deppe, 1830), and bare-throated tiger heron, *Tigrisoma mexicanum* Swainson, 1834, preying on hatchlings in the first, second, and third month after hatching (couple sightings per month). Cannibalism was not observed.

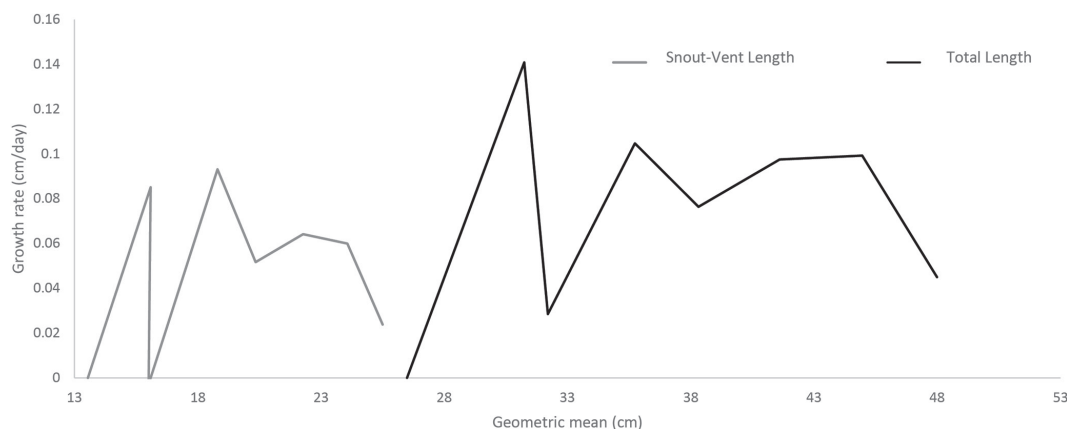
Regarding the population model, in the first case (live recapture), survival-recapture probabilities time-dependent ( $\phi(t)$ ,  $p(t)$ ) was the most accurate model to describe the data (AICc = 138.39, model likelihood = 1.0, number of parameters = 12). In the second case (Popan formulation) the survival time dependent recapture-entrance constant ( $\phi(t)$ ,  $p(\cdot)$ ,  $pent(\cdot)$ ,  $N(\cdot)$ ) was the most accurate model to describe the data (AICc = 170.39, model likelihood = 1.0, number of parameters = 10). Hatchling population size was estimated to be 218.6 ± 31.9 SE hatchlings in ca. 22.4 km<sup>2</sup> (from Boca Grande to Punta Felipa, 4.5% of Coiba Island area; 95% confidence interval, lower bound = 164.4; upper bound = 290.6). Based on that model, the hatchling population estimated for each recapture period was 187.3 ± 9.1 SE hatchlings in May, 64.2 ± 14.7 SE in June, 7.6 ± 4.1 SE in July, 3.3 ± 1.7 SE in August, 4.2 ± 1.9 SE in September, 5.1 ± 2.2 SE in October, 6 ± 2.5 SE in November, and 0.8 ± 0.5 SE in December. The hatchling population decline rate was of 65.7% in May–June and 95.9% in July, with only 0.5% of this population surviving through December (Fig. 7).

## DISCUSSION

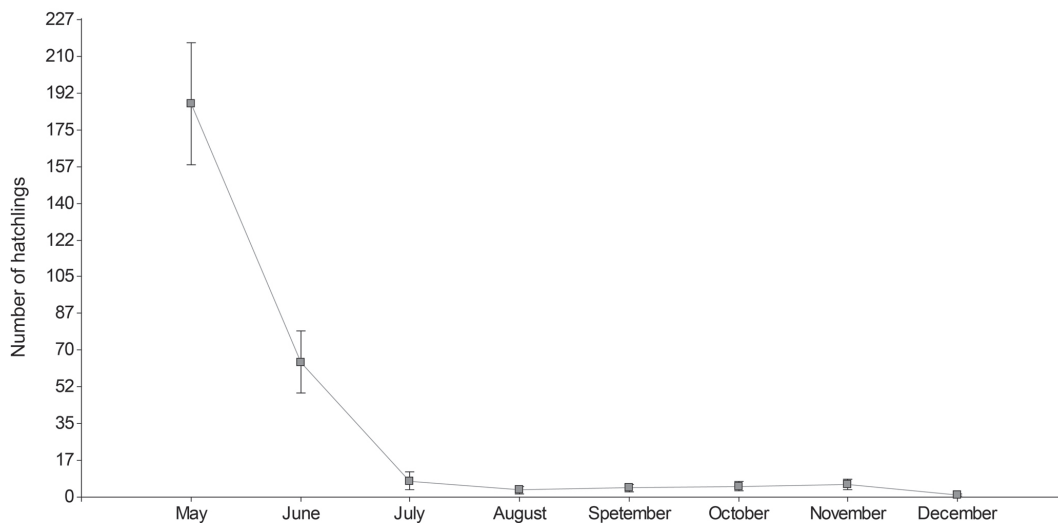
This is the first study to assess the biological, physical, and chemical conditions of American crocodile nesting areas in the Pacific, as well as hatchling growth rates. In contrast to the lack of information from the Pacific, information about nesting and reproductive ecology in the Caribbean has been obtained in coastal habitats (Ogden, 1978; Mazzotti, 1983; Platt and Thorbjarnarson, 2000b), atolls (Charruau et al., 2010; Platt and Thorbjarnarson, 2000b), some islands (Varona, 1980; Medem, 1981; Thorbjarnarson, 1988, 1989), and at mainland sites (Medem, 1981; Espinal and Escobedo-Galván, 2010; see Table 4). Comparing our results with these studies, the mean clutch size on Coiba (25.2 ± 9.5 eggs) was not significantly different (one-sample  $t$ -test,  $P = 0.18$ ) from those reported from mainland Panama (46 eggs, Breder, 1946), Mexico, Banco Chinchorro (16.2 ± 4.6 eggs, Charruau et al., 2010), Belize (22.3 ± 6.0 eggs, Platt and Thorbjarnarson, 2000b), Haiti (22.5 ± 2.7 eggs, Thorbjarnarson, 1989), Florida, USA (45.2 ± 17.2 eggs, Ogden, 1978; 38.0 ± 0.4 eggs, Kushlan and Mazzotti, 1989), or in two Colombian populations (mainland 40–60 eggs, Fuerte Island 18–20 eggs; Medem, 1981; Table 4). However, we observed that the mean clutch size of *insular* populations on Fuerte Island



**Figure 5.** Hatchling-juveniles growth registered throughout nine months (April to December). A nonlinear regression test determined that Gompertz's model best describes growth in that period (all terms of the model contributed significantly,  $P < 0.05$ ).



**Figure 6.** Total length and snout-vent length growth rates of hatchlings from April–December, 2013. We used eight of the nine months to calculate the geometric mean and the growth rate, excluding November, because that was just one datum and an outlier.



**Figure 7.** Hatchling population size estimated for each recapture event over nine months (April–December) on Coiba Island based on the Popan formulation model.

**Table 4.** Some variables assessed in other studies on nesting ecology of *Crocodylus acutus* at insular and mainland localities. MRS-TL: Minimum reproductive size defined as total length, CS: Clutch size, EM: Egg mass, EL: Egg length, EW: Egg width, NS: Nesting success, DT: Depth to the top of the clutch, DB: Depth to the bottom of the clutch, WD: Width of hole, VWC: Volumetric water content.

Author	Country	MRS-TL (m)	CS	EM (g)	EL (mm)	EW (mm)	NS (%)	DT (cm)	DB (cm)	WH (cm)	VWC (%)
Current study	Panama (Isla Coiba)	2.09 female	25.2 ± 9.5	97.1 ± 4.3	74 ± 4	40 ± 7	88.9	17.5 ± 7.8	42.9 ± 9.9	35.9	24.56 ± 8.80 bottom 20.94 ± 8.48 middle
Breder (1946)	Panama (mainland)		46								
Alvarez del Toro (1974)	Mexico	2.8 female									
Klein (1977)	Honduras	2.4 female									
Ogden (1978)	USA, Florida		45.2 ± 17.2								
Varona (1980)	Cuba	2.7–3.0 female									
Medem (1981)	Colombia (mainland)	2.19 male	Between 40 and 60								
		2.36 female									
Medem (1981)	Colombia (Fuerte Island)		Between 18 and 20								
Mazzotti (1983)		2.25 females									
Thorbjarnarson (1988, 1989)	Haiti	2.2–2.3 females	22.5 ± 2.7								6.6 ± 3.1
Kushlan and Mazzotti (1989)	USA, Florida		38 ± 9.4								
Platt and Thorbjarnarson (2000)	Belize	≤ 2 m females	22.3 ± 6.0	85.6 ± 9.7	70.5 ± 4.3	44.1 ± 1.6	80	23.3 ± 6.3	32.8 ± 5.4	26.0 ± 8.6	
Charruau et al. (2010)	Mexico (Banco Chinchorro)	1.94 m females	16.2 ± 4.6	80.0 ± 7.2	69.3 ± 3.4	43.3 ± 1.6	73.2	17.7 ± 5.5	32.8 ± 5.6	24.0 ± 5.6	0.11 ± 0.07

(18–20 eggs), Banco Chinchorro (16.2 ± 4.6 eggs), Haiti (22.5 ± 2.7 eggs) and Coiba Island (25.2 ± 0.5 eggs) was lower than for mainland populations in Colombia (40–60 eggs), Florida (38.0 ± 9.4 eggs), and Panama (46 eggs), which might result from the smaller body size of reproductively mature females on islands (Platt and Thorbjarnarson, 2000b). Clutch size is positively correlated with female body size (Platt and Thorbjarnarson, 2000b). In general, 19 eggs have been reported as the minimum number in American crocodile nests (Ferguson, 1985) but studies at Banco Chinchorro (16 eggs), Fuerte Island (18 eggs), and Coiba (16 eggs) show that this value can be lower and depends on the minimum reproductive size (MRS) of the female.

There is no consensus about what the MRS is for either female or male *Crocodylus acutus*, but it is likely to vary throughout the range of the species (Thorbjarnarson, 1989). Currently, the MRS for mainland males and females is known from American crocodiles in Colombia (a captive male of 219 cm TL mated with a female of 236 cm TL; Medem, 1981) and Florida, USA (estimated to be 225 cm TL for females; Mazzotti, 1983). The MRS is known for island crocodile populations in Haiti (Etang Saumatre, females begin nesting at around 220–230 cm TL; Thorbjarnarson, 1988), Mexico (Banco Chinchorro, 194 cm TL female; Charruau et al., 2010), and Belize (Turneffe Island, ≤ 200 cm; Platt and Thorbjarnarson, 2000b), which have the smallest MRS. Other reports of female American crocodile MRS on the mainland are from Honduras (240 cm TL: Klein, 1977), Cuba (270–300 cm; Varona, 1980), and Mexico (280 cm; Alvarez del Toro, 1974; Table 4). The female MRS recorded on Coiba was 209 cm, which is comparable to the female MRS reported from other insular populations in the Caribbean. This is likely to be due to genetic, environmental, or behavior factors (Thorbjarnarson, 1988; Platt and Thorbjarnarson, 2000b; Charruau et al., 2010). Additional pressures that have been suggested to lead to smaller female insular MRS include lack of resources (food, space, freshwater, etc.) or even concentrated overharvesting (Platt and Thorbjarnarson, 2000b).

Mean egg mass, depth to the bottom of the clutch, width of nest, and egg length in Coiba Island crocodiles (Table 2) were higher than in Belize (85.6 ± 9.7 g; 32.8 ± 0.4 cm; 26.0 ± 0.6 cm; 70.5 ± 0.3 mm; Platt and Thorbjarnarson, 2000b) and Banco Chinchorro Atoll (80.0 ± 7.2 g; 32.8 ± 0.6 cm; 24.0 ± 0.6 cm; 69.3 ± 0.4 mm; Charruau et al., 2010; see Table 4). Otherwise, mean depth to top of the clutch, distance to water, and egg width in Coiba were lower than Banco Chinchorro (17.7 ± 5.5 cm; 1,990 ± 810 cm; 43.3 ± 1.6 mm; Charruau et al., 2010), Belize (23.3 ± 6.3 cm; distance to water unknown; 44.1 ± 1.6 mm; Platt and Thorbjarnarson, 2000b), and Haiti (no depth to top; 2,750 ± 1,180 m; egg width unknown; Thorbjarnarson, 1988).

Volumetric water content (VWC) was measured by Thorbjarnarson (1989) and Charruau et al. (2010) in Haiti and Banco Chincorro Atoll, with mean values of  $6.6 \pm 3.1\%$  and  $0.11 \pm 0.07\%$ , respectively. These values are lower than what we estimated on Coiba Island (nest 1 and nest 2:  $25.44 \pm 6.34\%$  and  $24.56 \pm 8.80\%$ , respectively, at nest bottoms;  $24.66 \pm 2.07\%$  and  $20.94 \pm 8.48\%$ , respectively, at the middle of the nest). Differences between nests 1 and 2 in Coiba Island may be related to the presence of canopy cover at the first nest and its absence at the second nest. We were not able to compare the soil chemical conditions to other localities because comparative data from other American crocodile nesting sites are unavailable.

Several authors report that in countries such as Mexico and Cuba females are territorial towards one another and often compete for nest sites (Alvarez del Toro, 1974; Varona, 1980). However, in other parts of its range, such as Florida, USA (Kushlan, 1982), Haiti (Thorbjarnarson, 1988), Dominican Republic (Thorbjarnarson, 1989), and Belize (Platt and Thorbjarnarson, 2000b), female crocodiles are apparently less territorial and may even nest colonially or in small groups. This latter behavior was observed in Coiba Island (distance between nests at Playa Blanca was  $620 \pm 30$  cm) and at two other nesting areas on the island (south of Playa Blanca and El Maria beach), where distances between nests were no more than 5,000 cm (1,300 cm between nest 8 and 9 and  $47.3 \pm 15.3$  m among nests 4, 5, 6, and 7). Although there were plenty of available (and seemingly suitable) beaches for nesting in Playa Blanca and El Maria, characteristics such as proximity to freshwater, elevation, and vegetation cover probably determine nest site selection.

Oviposition in Coiba occurred during the dry season (January) and hatching was during the beginning of the rainy season (April), consistent with observations by Breder (1946) on crocodiles from mainland Panama and by Thorbjarnarson (1989) and Medem (1981) for *Crocodylus acutus* in Central America, South America, and on Caribbean Islands. The length of incubation in Coiba (Table 2) was comparable to those reported by Varona (1980) in Cuba (80–90 days), Kushlan and Mazzotti (1989) in Florida (85 days), Alvarez del Toro (1974) in Mexico (80 days) and Thorbjarnarson (1989) on Dominican Republic (84 days). Alvarez del Toro (1974) and Varona (1980) reported that oviposition can follow courtship by 1 or 2 months, and gravid females begin to visit potential nesting areas 4–6 weeks before laying the clutch (Thorbjarnarson, 1988). Courtship activity on Coiba most likely starts in November and females visit potential nest sites in December. We did not observe any agonistic behavior or courtship activity in coastal areas. It is highly probable that any such events happened in internal water bodies (mangroves or close rivers and creeks) where we did not survey.

Parental behaviors were observed during both nesting and hatching periods. We gathered information about continued nocturnal visits of mothers to nests throughout the nesting period, revealing active nocturnal parental care. We did not encounter nest defense behavior toward researchers during the day over the nest, likely due to low diurnal activity in those areas. Some authors report that such behavior is common in places in inland Panama (Dugan et al., 1981), Mexico (Alvarez del Toro, 1974), and Cuba (Varona, 1980). On the other hand, at Florida, USA and Haiti it has been reported that females provide little or no nest protection (Ogden, 1978; Thorbjarnarson, 1988; Platt and Thorbjarnarson, 2000b). After hatching there was a short period (2–3 weeks) with parental care (adults in the water with hatchlings responding to distress calls), but once hatchling-juveniles started to disperse from the nurseries adults were no longer observed in the area. This lack of extended maternal behavior period in the American crocodile has also been reported in Panama (Rodda, 1984), Haiti (Thorbjarnarson, 1988), Florida, USA (Kushlan and Mazzotti, 1989), and Belize (Platt and Thorbjarnarson, 2000b). Coiba Island was a prison from 1919–2004, when it finally closed (Ibáñez, 2011). This suggests that coastal crocodile populations were probably subjected to hunting for a long time and were displaced to inland areas not inhabited by humans. Therefore, we might be witnessing population expansion or a re-colonization of suitable habitats where this species occurred historically.

Natural hatching success in Coiba was highly variable among females (6.3–100%), likely due to differences in female size and behavior. On average, Coiba had lower natural hatching success (68.3%) compared to other insular and coastal localities such as Banco Chincorro (73.2%) and Belize (80.0%). On five occasions, after mother crocodiles left the nest, we found eggs piping and hatchlings trying to dig towards the surface, which, without our aid, probably would have died. Therefore, it is likely that the low hatching success is not primarily due to external conditions or predation, as has been commonly reported elsewhere (Mazzotti, 1999), but due to differences in parental behavior. For example, in one nest the female helped only a single hatchling, leaving the others inside the nest. This minimal level of parental investment might be correlated with overharvesting in the past, which can reduce the amount of observed parental care (Thorbjarnarson, 2010).

Habitats in nesting areas showed evidence of ecosystems in the process of restoration, probably since 2004 when the prison on Coiba was formally closed. A mosaic of dry, riparian, and mangrove ecosystems are the result of anthropogenic impacts (Ibáñez, 2011). Based on information collected from people that worked in the area until the prison was closed (pers. com.), crocodiles were not commonly seen nesting in or around our study sites.

We caught newly hatched hatchlings on Coiba with a minimum size of 25 cm TL, 11.90 cm SVL, and 40 g. These values were lower than the values reported by Platt and Thorbjarnarson (2000b) in Belize (one-week-old hatchling minimum TL = 26.2 cm, SVL = 12.4 cm, mass = 46 g) and greater than those reported by Charruau et al. (2010) in Banco Chinchorro (minimum = TL 23 cm, SVL = 11.5 cm, mass = 30 g) and Thorbjarnarson (1988) on Haiti (TL 24.4 cm). Growth rates for hatchlings on Coiba ranged between 0.03 and 0.16 cm/day compared to  $0.13 \pm 0.04$  cm/day for hatchlings from Haiti over the first 65–86 days (Thorbjarnarson, 1988). On the other hand, few studies on survival rates have been carried out for *Crocodylus acutus* hatchlings. We found a high hatchling population decline rate during the first 2 months and a lower decline rate following those months until the eighth month. For crocodiles in general, apparently the first 2–3 months are critical, and nursery habitats play an important role in hatchling survival (Thorbjarnarson, 1889). We found early dispersal of these hatchlings ( $0.017 \pm 0.033$  km after first month since hatching), likely related to the low cover of the nursery areas (mainly mangrove and riparian forest in regeneration) and the high number of predators (mainly large fishes, sharks, and birds) present.

Based on the mean nest size on Coiba ( $25.2 \pm 4.3$  eggs) and the hatchling population estimates ( $218.6 \pm 31.9$  SE), a plausible number of nests for this area in 2013 could be  $8.7 \pm 0.8$ . We found 10 nests, which is very similar to the number of nests estimated for the gross population based on mark-recapture analysis. This suggests that we likely found most, if not all nests in that area.

Our results suggest that availability of suitable nursery areas in Coiba might be playing a more important role in the population growth of American crocodile than physical conditions. Although we did not assess these habitats in depth, the presence of human impacted ecosystems in the process of regeneration and personal observations about predation might be related to the low hatchling survival rates.

In conclusion, American crocodile reproductive ecology on Coiba Island showed patterns more closely related to insular habitats in the Caribbean islands than to mainland areas. Although some topics such as courtship and mating will require more research to determine where, when, and which variables might influence these behaviors, we obtained a good glimpse into nesting and hatching behavior. The low incidence of infertile, dead, and unhatched eggs and predation suggest that nesting beaches on Coiba are characterized by optimal conditions to carry on successful nesting. However, minimal parental care might play an important role in the low hatching success that we observed. There is still very little information about survival rates of hatchlings in this species; however, we think that the low number and poor quality of nurseries on Coiba's coastal line are correlated with

early hatchling dispersal to the exposed areas (beaches, sea, and rocky coastline) and the low survival rate after 9 months. For this reason, habitat conservation plans and in-depth research on the relationship(s) between habitat conditions and demography of this species should be a priority in future conservation management plans on Coiba Island.

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## ONLINE SUPPORTING MATERIAL

The following Supporting Information is available for this article online:

**Video S1.** Hatching process in an American crocodile nest on Coiba Island. Notice how the mother aids hatchlings by digging and breaking shells to help them emerge.