**Report to the IUCN-SSC Crocodile Specialist Group**

**Student Research Assistance Scheme (SRAS)**

# Study of the reproductive effort of females *Crocodylus acutus* in Banco Chinchorro atoll, South East Mexico

**by**

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Septembre 2022

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As part of my studies and my professional development, I chose to take a sabbatical year between my first and second year of my master's degree. This time allowed me to take a step back in my professional desires. I was not sure about continuing in the research sector (I had followed up on the blue tit and the big tit during my first year of my master's degree) and I had no idea what I really wanted. So I decided to do another internship based on a different research project: the monitoring of American crocodile reproduction from Banco Chinchorro, México. The goal was to make sure the path I was going to take in my studies was the right one.

This American crocodile monitoring project is directed by Dr. Pierre Charruau, crocodile specialist at the Centro del Cambio Global y la Sustentabilidad A.C. (Villahermosa, Tabasco, Mexico) and member of the CSG. Dr. Charruau accepted me as a fellow, but he could not pay me for the work I could do. However, he told me that I could apply for the CSG student research assistance scheme. Obtaining this grant allowed me to pay for my 4-month stay in Mexico and to work with Dr. Charruau. During this time, we wrote a scientific paper on the breeding effort of Banco Chinchorro crocodiles. For that, I compiled the known information on this topic, participated in the 2019 fieldwork campaign and analyzed the data collected by Dr. Charruau and his colleagues from 2006 to date on the reproductive parameters of *Crocodylus acutus* at Banco Chinchorro. We managed to estimate the reproductive effort of females and the reproductive frequency of female crocodiles from Banco Chinchorro based on data from 2006 to 2019.



***Capture of an American crocodile at Banco Chinchorro. Mexico (May 2019)***




***A small clutch of Crocodylus acutus found in May 2019 at Banco Chinchorro, Mexico.***

The article "Reproductive dynamics of an isolated population of American crocodiles (*Crocodylus acutus*) based on long-term monitoring data" was published in the Journal of Herpetology, with the participation of Pierre Charruau, David Ichbia, Giovany A. Gónzalez-Desales, and Steven G. Platt (see PDF of the attached article). Two years ago, I graduated from the Master of Biodiversity, Ecology and Evolution of the Université Paris-Saclay (Paris, France), and I am now working as a botanist in a French association. I would like to thank the Crocodile Specialist Group for awarding me the scholarship. It allows me to work in another research program and helped me to find my professional desire.

The work done during my stay in Mexico is presented below.

# Reproductive Dynamics of an Isolated Population of American Crocodiles (*Crocodylus acutus*) Based on Long-term Monitoring Data

**ABSTRACT.**—The American crocodile (*Crocodylus acutus*) is still considered Vulnerable, with some populations remaining depressed and showing little evidence of recovery. An understanding of its reproductive dynamics and parameters is essential for its conservation and management. Although the knowledge of *C. acutus* reproductive ecology has greatly increased during recent years, some critical parameters such as breeding effort (i.e., proportion of adult females that nest each year in a population) remain poorly known. Herein we analyzed 14 years of reproductive data from a *C. acutus* population in a Mexican atoll to better understand its reproductive dynamics in space and time. We estimated the number of reproductive females in the population and in each nesting area, compared nest characteristics and clutch parameters among nesting areas, and determined female breeding effort and breeding frequency (i.e., proportion of years that an adult female nested). We estimated that 35 reproductive female *C. acutus* inhabit the main island of the atoll, distributed among 12 nesting areas. The annual female breeding effort ranged from 27.3 % to 60.6 % and the breeding frequency of 15 selected females ranged from 57.1 to 92.3 %. Breeding effort depends on the breeding effort in preceding years. We also found significant differences in reproductive attributes (i.e., number of nests, nest-water distance, nest depth, clutch size, and nesting success) among nesting areas that we explain by the quality of those habitats for crocodile nesting and territorial behavior of females.

The American crocodile (*Crocodylus acutus*) occurs from the southern tip of Florida, USA to northern South America (Rainwater et al., 2021). Many populations throughout this range are threatened by habitat loss and degradation, accidental entanglement in fishing nets, illegal hunting, and hybridization with sympatric Morelet´s crocodile (*Crocodylus moreletii*) and Cuban crocodile (*Crocodylus rhombifer*) (Rainwater et al., 2021). Although populations in some areas have recovered from past perturbations and are now stable or increasing, others remain depressed with little evidence of recovery (Charruau et al., 2005; Thorbjarnarson et al., 2006; Rainwater et al., 2021). *Crocodylus acutus* is considered Vulnerable by the IUCN (Rainwater et al., 2021), and populations of Mexico are listed on Appendix II of CITES (2020).

An understanding of reproduction in *C. acutus* is essential for biologically-based population management and conservation. During the last two decades the knowledge of *C. acutus* reproductive ecology has greatly increased (Platt and Thorbjarnarson, 2000; Mazzotti et al., 2007; Charruau et al., 2010; 2011; 2018; Balaguera-Reina et al., 2015; Gónzalez-Desales et al., 2016; Gómez-Gonzáles et al., 2017); however, although crocodiles are known iteroparous reptiles there is a notable paucity of information on female breeding effort (i.e., the proportion of females in a population that reproduce each year; Thorbjarnarson, 1989), and this critical demographic parameter remains unknown for most populations. Only three studies determined this parameter for populations of *C. acutus*; one in Haiti (Thorbjarnarson, 1988) and two in Florida, USA (Kushlan and Mazzotti, 1989; Wasilewski and Enloe, 2006). These studies determined values of 72 % and 50 % (Florida), and 63.8 % (Haiti) which are within the range of published values for other crocodilians (<10–90 %, Thorbjarnarson and Wang, 2010). Female breeding effort is not well-understood in crocodilians, and appears to be energy-limited, and is likely dependent on physiological, nutritional, and environmental conditions (Thorbjarnarson, 1994, Elsey, 2006; Elsey et al., 2008; Platt et al., 2008; Thorbjarnarson and Wang, 2010). Furthermore, there is no published data on the breeding frequency of female *C. acutus* (i.e., proportion of years that an adult female nested).

Mexican populations of *C. acutus* were recently transferred from Appendix I to Appendix II of CITES (CITES, 2020) with the intention of developing a sustainable harvest program, as the next step in the recovery of these populations. A thorough understanding of the reproductive ecology of female *C. acutus*, including their annual breeding efforts, is therefore critical to designing sustainable egg harvest or sound management programs.

Long-term monitoring of populations permits the study of life history parameters that vary through time and the variables affecting them (Clutton-Brock and Sheldon, 2010). The importance of long-term studies to test ecological and evolutionary questions is well-known. Furthermore, long-term studies can identify and resolve environmental issues at all scales (Franklin, 1989; Clutton-Brock and Sheldon, 2010). In 2003, we began monitoring American crocodiles in the Banco Chinchorro Atoll, Mexico, and, have studied the reproductive dynamics of this population since 2006 (Charruau et al., 2005; Charruau et al., 2010). The primary objective of this study is to analyze 14 years of reproductive data from the population of *C. acutus* in Banco Chinchorro to better understand the reproductive dynamics of this population in space and time. Our specific

objectives were to 1) estimate the number of reproductive females in the population and in each nesting area, 2) compare nest characteristics and clutch parameters among nesting areas and 3) determine female breeding effort and breeding frequency.

## MATERIAL AND METHODS

***Study Area***.—We conducted our study in the Banco Chinchorro Biosphere Reserve, an offshore atoll located 31 km southeast of the State of Quintana Roo, in Mexico. The atoll contains four islands (Cayo Lobos, Cayo Centro, Cayo Norte Menor and Cayo Norte Mayor), of which Cayo Centro is by far the largest (541 ha), and situated at 50 km from the nearest point on the Quintana Roo coast. This island is characterized by mangrove and halophytic or coastal dune vegetation and several hypersaline (30 to 65 ppt) lagoons are present in the interior (Charruau et al., 2005; Charruau et al., 2010). The climate of Banco Chinchorro is warm-subhumid with rains in summer and winter (Instituto Nacional de Ecología [INE], 2000; Charruau et al., 2010). Maximum precipitation occurs during October-November and minimum during March-April; the coldest and warmest months are December-January and July-August, respectively (Charruau et al., 2010). The physiography of the biosphere reserve is described in much greater detail elsewhere (INE, 2000).

*Data Collection.*—We conducted our study in May (egg-laying season) and August (hatching season) of each year from 2006 to 2019. During the egg-laying season we inspected known and potential nesting areas on foot and searched for tracks and evidence of digging to detect nests. We recorded geographic coordinates (datum WGS84) of each nest using a Global Positioning System (GPS) with a maximum precision of ±3 m. We carefully excavated each nest to determine the clutch size and then used a pencil to mark the uppermost surface of each egg in order to maintain its upright orientation when replaced in the nest (Charruau al., 2010; Charruau, 2012). We evaluated egg viability by the presence of opaque bands on the eggshells (Ferguson, 1985). We measured (±1 cm) the distance from the edge of the nest hole to water (nest-water distance) and depth to the bottom of the clutch (nest depth). We obtained nest temperatures with data loggers [HOBOs Temperature/light (waterproof) UA-002-08; Onset Comp. Corp., Bourne, MA, USA]. We placed the data loggers in the middle of the clutch and programmed them to register temperature every 30 minutes until hatching (Charruau et al., 2010; Charruau, 2012). In August (hatching season), we revisited all of the nests found during the egg-laying season to determine their fate and to recover data loggers. We considered a nest successful when at least one living

neonate emerged from it. We also closely inspected all nesting areas to detect any hatched nests over-looked during the egg-laying season. We determined the coordinates and measured the distance to water of any over-looked nests.

***Data Analysis***.—We used Google Earth Pro to visualize the position of all nests and determine nesting areas. We defined nesting areas as continuous homogeneous habitat segments that contained one or more nests. We determined the mean ± 1 SD and intervals (minimum-maximum) of clutch viability (%), clutch temperature (°C), nest-water distance (m), nest depth (cm) and clutch size (number of eggs) for each nesting area. We also determined the nesting success of each area as the percentage of successful nests. We calculated the percentage of active nesting areas (where nests were present) by year and the percentage of years with at least one nest for each area. We determined the maximum number of reproductive females for each nesting area as the maximum number of nests in a single year for each area. We then calculated the annual breeding effort as the percentage of females that nested each year.

As female American crocodiles in Banco Chinchorro are known to return to the same geographic location to nest (Charruau et al., 2010), clusters of nest points from different years with the same geographical location were considered to be from the same female. We selected 15 clusters of nest points with a minimum of 5 years of data to calculate the breeding frequency (the proportion of years that an adult female nested) of 15 females, through nest site fidelity.

*Statistical Analysis.*—We conducted statistical analyses in R version 1.1.383 (RCore Team, 2017) and RStudio 1.3.159 (RStudio Team, 2020). We analyzed normality with Shapiro tests. We used a Kruskal-Wallis test to compare nest parameters among nesting areas and a post hoc Kruskal Multiple comparison (kruskalmc) test using the package pgirmess to determine which areas differed from others. Nesting success is a binary variable, so we used a Fisher test to determine if differences existed among nesting areas, then applied a post hoc Fisher multiple comparison (fisher.multcomp) test, with the RVAideMemoire package, to compare areas. We performed a regression analysis between breeding effort and mean breeding effort of the preceding one to six years. We considered the results significant at $P < 0.05$.

## RESULTS

We located 181 crocodile nests at 12 nesting areas during the 14 years of our study (Figs. 1, 2). One nesting area (III) found in 2006 was not revisited until 2019 because of damage caused by

Hurricane Dean and is no longer considered suitable for nesting. We visited nesting area VIII each year beginning in 2006, although nests were not found here until 2019. Based on clutch size (9 eggs) the recent nest found in this area most likely belongs to a young female (Table 1). We found a mean of 12.9 ± 3.7 nests/year with a minimum of 8 in 2007 and a maximum of 20 in 2018 (Fig. 2). Fifty to 100 % of the nesting areas were active each year and individually, nesting areas were active from 53.8 to 100 % of the years (Table 2).

We estimated that 35 reproductive females could occur on Cayo Centro based on location of nests (Table 2). We estimated a mean annual female breeding effort of 44.6 % ranging from 27.3 to 60.6 % annually (Table 2). We estimated the breeding frequency of 15 females to range from 57.1 to 92.3 % (Table 3) with a mean of 65.8 %. The females exhibited one to three consecutive years without reproduction, and one to ten consecutive years with reproduction (Table 3). We initially found no significant relationships between annual breeding effort and breeding effort of the preceding year or the mean breeding effort of the two to six preceding years. However, after deleting atypical data suggested by the program, we found two significant negative relationships (Fig. 3); between annual breeding effort and mean breeding effort of the two preceding years ($F_{1, 9}$ = 7.44; P = 0.023), and mean breeding effort of the four preceding years ($F_{1, 7}$ = 6.40; P = 0.039). Relationships between annual breeding effort and mean breeding effort of the precedent year ($F_{1, 10}$ = 4.02; P = 0.072), three ($F_{1, 8}$ = 0.95; P = 0.358), five ($F_{1, 6}$ = 0.34; P = 0.583), and six precedent years ($F_{1, 6}$ = 0.86; P = 0.388), were not significant.

Nesting areas III and VIII were not included in the parameter analyses among areas because area III contained only one nest and became a non-nesting zone following Hurricane Dean until 2019 when only one nest was found at area VIII. Mean number of nests per year differed significantly among nesting areas (Kruskal-Wallis Chi-square = 50.831, df = 9, P = 7.515e-8). A greater number of nests per year occurred at nesting area I in comparison to nesting areas IV, VI, VII, IX, X, XI, and XII (Table 1; kruskalmc, P < 0.05). There were no differences in clutch viability (Kruskal-Wallis Chi-square = 3.0191, df = 9, P = 0.9635) and clutch temperatures (Kruskal-Wallis Chi-square = 14.865, df = 9, P = 0.09472) among nesting areas (Table 1). We found significant differences in nest-water distance among nesting areas (Kruskal-Wallis Chi-square = 20.326, df = 9, P = 0.016). Nests in nesting area I were further from water than nests in nesting areas V, VII, IX and X; nests in nesting area II were further from water than nests in nesting areas V and X; and nests in nesting area XII were further from water than nests in nesting areas V, IX and X (Table 1;

kruskalmc, $P < 0.05$). We also found differences in depth to the bottom of the nest among areas (Kruskal-Wallis Chi-square = 22.611, df = 9, P = 0.007132). Nests in nesting areas I and IX were deeper than nests in nesting area XII (Table 1; kruskalmc, $P < 0.05$). Clutch size also differed among nesting areas (Kruskal-Wallis Chi-square = 36.134, df = 9, P = 3.754e-5). Mean clutch size was greater in nesting area I than in nesting areas II and V; and nesting area XII had a greater mean clutch size than nesting area II (Table 1; krukalmc, $P < 0.05$). Nesting success also varied significantly among areas (Fisher test, P = 0.0004998). Nesting success was higher in nesting area I than in nesting areas IV, V, VII and IX, while nesting area XI had higher nesting success than nesting area V (Table 1; fisher.mutlcomp, $P < 0.05$).

## DISCUSSION

We estimated that 35 reproductive female *Crocodylus acutus* inhabit Cayo Centro, Banco Chinchorro atoll, distributed among 11 currently active nesting areas. The maximum of 20 nests found in 2018 lends confidence to our estimate of females inhabiting the island. During our study, the number of nesting areas increased over time with a new site discovered in 2019. Thus, we cannot be certain that all nesting areas on the island have yet been identified. Tellingly, *C. acutus* is a very adaptable crocodilian that exhibits flexible nesting behavior with some individuals constructing mound nests of sand or peat and others excavating typical hole nests (Thorbjarnarson, 1989). Because mound nesting is known to occur in the reserve (Charruau et al., 2010) we cannot rule out the possibility that some females nest in isolated sites in the mangroves where they are likely to escape our notice (see also Platt and Thorbjarnarson, 2000).

To our knowledge, this is the fourth study (see also Thorbjarnarson, 1988; Kushlan and Mazzotti, 1989; Wasilewski and Enloe, 2006) to estimate breeding effort of female *C. acutus* and appears to be the first to determine breeding frequency of some females. Our estimate is lower than those previously reported for *C. acutus*, but within the range of female breeding effort determined in other crocodilians (Thorbjarnarson, 1988; Kushlan and Mazzotti, 1989; Wasilewski and Enloe, 2006; Thorbjarnarson and Wang, 2010). The variation in annual breeding effort primarily depends on individual breeding frequency which in turn depends on female age/size, available resources, and climatic events. Our results suggest that some females reproduce 5–6 times during a single decade with other females reproducing almost annually. The reasons underlying this variability are poorly understood, but there is likely a complex interaction between the environment, nutrition,

and physiology of females (Lang, 1987; Nichols, 1989; Kushlan and Jacobsen, 1990; Elsey et al., 2008; Platt et al., 2008).

We found that annual breeding effort depends on the mean breeding effort during the preceding two and four years; meaning that the higher the percentage of females reproducing for two or four years in a row, the lower the percentage of females that reproduce during the third and fifth year. This could be related to the variability of ecosystem food resources, as this factor has been shown to significantly influence reproductive attributes of *C. acutus* (González-Desales et al., 2016). In addition, hurricanes can negatively affect aquatic ecosystems and in previous studies we demonstrated significant positive and negative effects of such climatic events on reproduction and body condition of *C. acutus* at Banco Chinchorro (Charruau et al., 2010; Labarre et al., 2020). In Banco Chinchorro food resources used by crocodiles for growth and reproduction are obtained mainly from the sea (Ávila-Cervantes et al., 2017). Therefore, future research should focus on the effects of food resources and hurricanes on breeding effort of female *C. acutus* at Banco Chinchorro.

According to Lang (1987), female breeding effort likely increases with size/age as crocodiles mature, and then declines late in life. In this study we were unable to obtain sufficient data on the size of reproductive females as they are elusive during the nesting season and difficult to capture. Moreover, we were reluctant to disturb females at nests and risk them abandoning their nests. Future research should seek to determine the sizes of reproductive females in the reserve to provide additional insights into reproductive dynamics.

Our results also show differences in several nest and clutch parameters among nesting areas. Female *C. acutus* carefully select nesting sites, using those most likely to ensure a successful outcome for their nest (Thorbjarnarson, 1989; Charruau et al., 2010). Furthermore, females can be territorial and compete with other females for nesting sites or exhibit minimal territoriality and nest colonially (Thorbjarnarson, 1989). In 2018 we observed nest site defense behavior by a nesting female (>2 m total length [TL]) toward other crocodiles approaching in the water close to the nest location (P. Charruau unpubl. data). Furthermore, on three occasions we found a number of eggs (15, 10 and 6) spread on the ground between the nest and the shore (P. Charruau unpubl. data). As no crocodile nest predators are present on the atoll (Charruau and Hénaut, 2012) that would likely result from agonistic encounters between nesting females (Alonso-Tabet et al., 2006), or from an unknown disturbance (e.g., human passing, first reproduction). These observations suggest that

territoriality and nest site competition among females could also be responsible for differences in nest and clutch parameters that we observed among nesting areas.

In general, nesting areas on the eastern side of the island (I, II, IX, X, XI and XII) show higher number of nests, greater nest-water distance, greater nest depth, larger clutch sizes, and increased nesting success in comparison to nesting areas on the western side of the island (IV, V, VI, and VII). This is not unexpected as the eastern side of Cayo Centro is the windward side and encompasses the most elevated terrain with an almost continuous sand ridge of 2–3 m asl and 30 to 60 m wide (INE, 2000). Nesting areas on this ridge are longer and wider than those present on the western side of Cayo Centro. In contrast, the western side (leeward side) of the island is characterized by lower terrain with smaller and more dispersed nesting areas. Thus, the eastern side of the island provides more suitable nesting habitat than western side and it is the former where the majority of females nest (138 nests vs. 36 nests) and where nesting success is greatest (66.8 % vs. 36.3 %). The elevated ridge of deep sand on the eastern side of the island also allows females to excavate deeper nest holes and position nests further from the water, thus lessening the chances of flooding by tidal over-wash.

Differences in the nest-water distance and clutch size between the eastern and western parts of the island could be due to the size of females nesting in those respective areas. The distance from the nest to the water represents a trade-off between flooding risk and the ability of the female to guard the nest. Nesting farther from the water reduces the likelihood of flooding while at the same time hampering the ability of the female to maintain surveillance of the nest. Moreover, as distance to water increases, so too does the time required for the female to transport neonates to the water and the longer neonates must remain in the nest and exposed to predators and scavengers (e.g., Platt et al., 2014) during hatching which may require several days (Charruau and Hénaut, 2012). In a previous study we found that smaller and presumably younger females nest further from the water than larger (and older) females (Charruau et al., 2010). Thus, older dominant females may exclude younger females from optimum nest sites causing them to nest further from the water on the eastern side of the island. The same is probably not possible on the western side owing to the reduced width of the only suitable nesting habitats. In the northern-most nesting area (IV), we found a mound nest containing two clutches in 2008 (Charruau et al., 2010), suggesting greater tolerance among nesting females in suboptimal nesting habitat where the likelihood of flooding is increased. Because clutch size is positively correlated to female body size in *C. acutus*

(Thorbjarnarson, 1996), our clutch size data indicates that more large females nest on the eastern than on the western side of the island.

In summary, we determined the number and breeding effort of reproductive females of *C. acutus* in Banco Chinchorro Biosphere Reserve, which is dependent on breeding effort during the preceding years. Food resources, tropical cyclones impacts, and size/age of females could also influence breeding effort but the role of those parameters has yet to be determined. We also found significant differences in reproductive attributes among nesting areas that are largely explained by the quality of those habitats for crocodile nesting and territorial behavior of females.

***Acknowledgments.***—This work was funded by the Centro del Cambio Global y la Sustentabilidad A.C. Second author obtained a grant from the IUCN-SSC Crocodile Specialist Group through the Student Research Assistance Scheme (SRAS). We are grateful to the Comisión Nacional de las Áreas Naturales Protegidas de México (CONANP) for its support in the field. We thank C. Peralta-Caretta for the elaboration of figure 1. Fieldwork was authorized by the Secretaría de Medio Ambiente y Recursos Naturales de México (SEMARNAT) with permit number SGPA/DGVS/03983/19.

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**Tables**

**Table 1.** Mean ± SD (n, minimum-maximum) of reproductive parameters of female *Crocodylus acutus* by nesting areas in Cayo Centro, Banco Chinchorro Atoll, from 2006 to 2019.

| Area | n nests | Clutch Fertility (%) | Clutch Temperature (°C) | Nest-Water Distance (m) | Nest Depth (cm) | Clutch Size | Nesting Success (%) |
|---|---|---|---|---|---|---|---|
| **I** | 4.1 ± 1.1 (14, 2-6) | 86.4 ± 9.2 (31, 63.6-100) | 31.9 ± 1.1 (32, 29.4-34.8) | 20.2 ± 7.8 (45, 10-41) | 32.8 ± 6.1 (42, 19-50) | 19.3 ± 5 (40, 10-30) | 83.9 (56) |
| **II** | 2.1 ± 1.1 (14, 0-4) | 84.7 ± 21.8 (13, 18.2 - 100) | 31.9 ± 0.8 (13, 30.2-33.0) | 16.8 ± 3.0 (16, 11-20) | 26.2 ± 6.1 (21, 16-42) | 12.2 ± 3.2 (20, 6-20) | 60.7 (28) |
| **III** | 1.0 (1) | - | - | 37 (1) | 35 (1) | 13 (1) | 0.0 (1) |
| **IV** | 0.7 ± 0.9 (13, 0-3) | 83.9 ± 10.7 (7, 63.6-95) | 30.8 ± 1.0 (3, 29.8-31.7) | 13.4 ± 3.4 (8, 10-19) | 29.7 ± 5.5 (7, 23-36) | 16.4 ± 5.2 (8, 10-24) | 22.2 (9) |
| **V** | 1.8 ± 0.5 (4, 1-2) | 51.6 ± 46 (3, 0.0-88.2) | 31.4 ± 0.9 (7, 30.1- 32.5) | 3.9 ± 1.9 (6, 2-7) | 22.3 ± 4.9 (7, 15- 30) | 11.4 ± 5.1 (7, 2-17) | 0.0 (7) |
| **VI** | 1.0 ± 0.0 (6, 1-1) | 86.5 ± 18.8 (3, 65-100) | 31.6 ± 0.9 (4, 30.9-32.9) | 5 (1) | 21.8 ± 7 (5, 13-29) | 19.0 ± 3.3 (5, 15-24) | 80 (5) |
| **VII** | 1.2 ± 0.8 (13, 0-3) | 89.8 ± 21.0 (8, 38.5-100) | 31.5 ± 0.7 (8, 30.5-32.4) | 10.4 ± 2.8 (9, 6-15) | 29.2 ± 3.5 (11, 23-36) | 15.6 ± 4.1 (14, 9-21) | 42.9 (14) |
| **VIII** | 1.0 (1) | 77.8 (1) | - | 0.3 (1) | 26 (1) | 9 (1) | 0.0 (1) |
| **IX** | 1.4 ± 0.7 (11, 1-3) | 81.3 ± 18.7 (9, 40-100) | 31.2 ± 0.8 (11, 30.3-32.4) | 9.9 ± 4.6 (13, 3-16.5) | 35.1 ± 5.8 (12, 29-47) | 17.2 ± 5.6 (13, 10-30) | 46.7 (15) |
| **X** | 0.9 ± 0.7 (14, 0-2) | 89.7 ± 9.4 (7, 77.4- 100) | 31.5 ± 0.4 (9, 30.9-32.1) | 8.6 ± 2.7 (11, 6-14) | 29.1 ± 5.7 (9, 22-40) | 16.3 ± 7.0 (11, 9-31) | 50.0 (12) |
| **XI** | 0.9 ± 1 (10, 0-3) | 87.8 ± 8.1 (6, 76.9- 100) | 30.7 ± 1 (6, 29.2- 31.8) | 14.8 ± 4.9 (7, 7.6-21.0) | 32.7 ± 4.1 (5, 28- 38.5) | 15.2 ± 2.5 (6, 12-19) | 88.9 (9) |
| **XII** | 1.3 ± 1.6 (13, 0-6) | 80.0 ± 17.6 (8, 52.9-100) | 30.9 ± 1.3 (8, 29.6-33.1) | 19.5 ± 8.4 (12, 3- 37.4) | 26.6 ± 4.5 (8, 22-37) | 18.8 ± 5.6 (10, 12-31) | 70.6 (17) |
| **Total** | 1.4 ± 0.9 (12, 0.7-4.1) | 84.4 ± 16.8 (96, 0-100) | 31.5 ± 1 (101, 29.2-34.8) | 15.4 ± 8.0 (130, 0.3-41) | 29.8 ± 6.6 (129, 13-50) | 16.5 ± 5.4 (136, 2-31) | 62.6 (174) |

**Table 2.** Maximum number of female (n max female) *Crocodylus acutus* by nesting areas in Cayo Centro, Banco Chinchorro Atoll and number of nests in each nesting area from 2006 to 2019 with the percentage of active year-by-area and active area-by-year. ABE: annual breeding effort. The dash means an absence of data for various reasons: we did not visit the area, the area was not discovered yet, or we lost the data. NC: not calculated because of lack of data.

| Nesting area | n max females | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2019 | % active year |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **I** | 6 | 4 | 4 | 4 | 5 | 4 | 6 | 3 | 5 | 4 | 2 | 6 | 3 | 3 | 4 | 100 |
| **II** | 4 | 1 | 1 | 2 | 2 | 2 | 3 | 1 | 3 | 4 | 0 | 4 | 2 | 2 | 2 | 92.9 |
| **III** | 1 | 1 | - | - | - | - | - | - | - | - | - | - | - | - | 0 | NC |
| **IV** | 3 | 1 | 0 | 3 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | - | 1 | 0 | 53.8 |
| **V** | 2 | - | - | - | - | - | - | - | - | - | 2 | 2 | - | 1 | 2 | NC |
| **VI** | 1 | - | - | - | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | - | 1 | 0 | 60.0 |
| **VII** | 3 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 0 | 3 | - | 2 | 0 | 84.6 |
| **VIII** | 1 | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | NC |
| **IX** | 3 | - | - | - | 1 | 1 | 2 | 1 | 3 | 1 | 1 | 2 | 1 | 1 | 1 | 100 |
| **X** | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 71.4 |
| **XI** | 3 | - | - | - | 1 | 0 | 3 | 1 | 1 | 1 | 0 | 0 | - | 2 | 0 | 60.0 |
| **XII** | 6 | - | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 1 | 2 | 0 | 2 | 6 | 1 | 69.2 |
| **Total** | 35 | 9 | 8 | 11 | 14 | 11 | 17 | 10 | 15 | 15 | 9 | 18 | 11 | 20 | 13 | |
| **ABE (%)** | | 47.4 | 33.3 | 45.8 | 45.2 | 35.5 | 54.8 | 32.2 | 48.4 | 48.4 | 27.3 | 54.5 | 52.4 | 60.6 | 38.2 | |
| **% active areas** | | 100 | 83.3 | 83.3 | 88.9 | 66.7 | 77.8 | 77.8 | 77.8 | 100 | 50 | 60 | NC | 100 | 63.6 | |

**Table 3**. Breeding frequency (%) of 15 selected female *Crocodylus acutus* in Cayo Centro, Banco Chinchorro Atoll. Data are presented as "0" absence of nest, "1" presence of nest and "-" lack of data.

| Nest ID | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 | 2018 | 2019 | breeding frequency |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **206** | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | - | 1 | 0 | 61.5 |
| **706** | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 71.4 |
| **506** | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 71.4 |
| **406** | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 57.1 |
| **606** | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 64.3 |
| **106** | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 57.1 |
| **306** | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 64.3 |
| **207** | - | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 92.3 |
| **108** | - | - | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | - | 1 | 0 | 63.6 |
| **408** | - | - | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 58.3 |
| **409** | - | - | - | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | - | 1 | 0 | 60.0 |
| **1409** | - | - | - | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | - | 1 | 0 | 60.0 |
| **209** | - | - | - | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 72.7 |
| **1514** | - | - | - | - | - | - | - | - | 1 | 0 | 1 | 1 | 0 | 1 | 66.7 |
| **1114** | - | - | - | - | - | - | - | - | 1 | 1 | 1 | 0 | 0 | 1 | 66.7 |

**Figure 1.** Map of Cayo Centro, Banco Chinchorro Biosphere Reserve, with nesting areas and location of nests (red points) of *Crocodylus acutus*. Data are from 2006-2019.

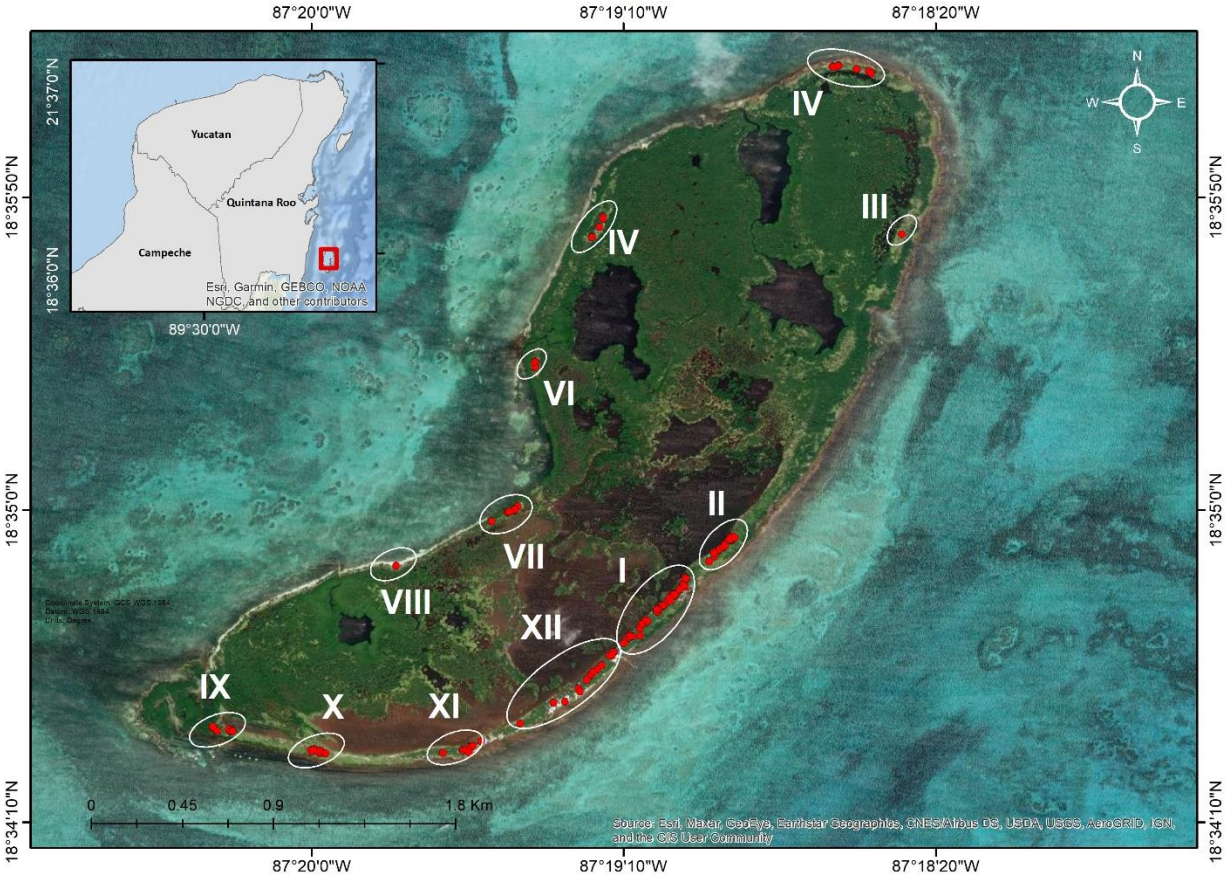



**Figure 2.** Number of crocodile nests found each year (bars) and cumulative number of nesting areas detected (line) in Cayo Centro, Banco Chinchorro Atoll from 2006 to 2019.

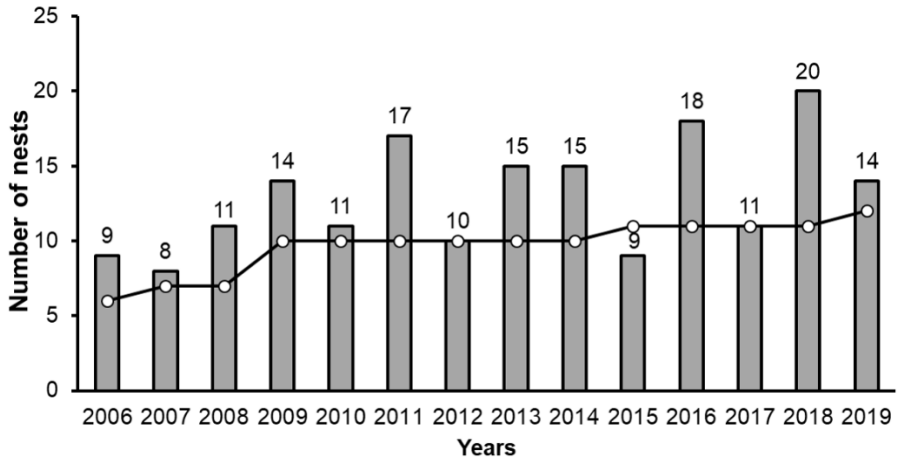


**Figure 3.** Graphics of simple regression analysis between female *Crocodylus acutus* mean annual breeding effort in preceding years (number of preceding years indicated above each figure) and annual breeding effort. Data are from 2006-2019.

