

Amphibia-Reptilia

Publication of the Societas Europaea Herpetologica



Co-Editors: Sebastian Steinfartz, *Braunschweig, Germany* and Judit Vörös, *Budapest, Hungary*.

Amphibia-Reptilia is a leading European multi-disciplinary journal devoted to most of the aspects of herpetology: ecology, behaviour, evolution, conservation, physiology, morphology, paleontology, genetics, and systematics.

Amphibia-Reptilia publishes high quality original papers, short-notes, reviews, book reviews and news of the Societas Europaea Herpetologica (SEH). The Societas Europaea Herpetologica (SEH) website is located at: www.seh-herpetology.org.

2016 Impact Factor: 1.287

5 Year Impact Factor 1.175.

 [Go to Online Edition](#)

 [Indexed by Web of Science](#)

 [Indexed by SCOPUS](#)

 [Read Free Sample Issue](#)

[Print Flyer](#)

[E-newsletters](#)

[more](#)



 Like 1



Tweet



ISSN:

0173-5373

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/305079600>

Nesting ecology of the American crocodile in La Encrucijada Biosphere Reserve, Mexico

Article in *Amphibia-Reptilia* · July 2016

DOI: 10.1163/15685381-00003051

CITATIONS

2

READS

304

4 authors:



Octavio Monroy-vilchis

Universidad Autónoma del Estado de México ...

79 PUBLICATIONS 584 CITATIONS

SEE PROFILE



Pierre Charruau

Centro del Cambio Global y la Sustentabilida...

51 PUBLICATIONS 177 CITATIONS

SEE PROFILE



Martha M Zarco-González

Universidad Autónoma del Estado de México ...

29 PUBLICATIONS 257 CITATIONS

SEE PROFILE



Giovany Arturo González-Desales

Universidad Autónoma del Estado de México ...

6 PUBLICATIONS 2 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Ecology and conservation of predators. [View project](#)



Vertebrates diversity of the Usumacinta river basin [View project](#)

All content following this page was uploaded by [Pierre Charruau](#) on 10 July 2016.

The user has requested enhancement of the downloaded file.

Nesting ecology of the American crocodile in La Encrucijada Biosphere Reserve, Mexico

Giovanly A. González-Desales¹, Octavio Monroy-Vilchis^{1,*},
Martha M. Zarco-González¹, Pierre Charruau²

Abstract. Nesting of the American crocodile (*Crocodylus acutus*) is affected by natural and anthropogenic processes. In Mexico, few studies exist on reproductive traits of wild populations. We assessed the key reproductive characteristics of *C. acutus* in the La Encrucijada biosphere reserve and the environmental and anthropogenic factors that influence them. From February to June 2014, we searched for nests in the reserve. Clutch incubation temperature was recorded by data loggers and climatic variables were obtained from La Encrucijada meteorological station. Additionally, outside the study area, net primary productivity was obtained for different sites in Mexico to relate it to clutch characteristics. We found 34 nests in nine nesting areas. Egg laying occurred in March, and hatching took place from mid-May to early June. Mean clutch and eggs characteristics are among the higher reported for *C. acutus*. Some egg attributes had a relationship with the net primary productivity. There was no relation between hatching success and external and internal characteristics of the nest. A high percentage of nests was poached (50%) mainly for egg consumption and fear of crocodiles, and the nests closer to the river, trees or human settlements are more likely to be poached.

Keywords: *Crocodylus acutus*, destruction of nest, nest poaching, reproductive biology.

Introduction

Three crocodylian species are present in Mexico (Instituto Nacional de Ecología, 2000) out of the 25 found in the world (Uetz and Hošek, 2014). Chiapas is the only Mexican state where the three species are naturally distributed: *Crocodylus acutus*, *Crocodylus moreletii* and *Caiman crocodilus chiapasius* (Álvarez del Toro, 1974; Instituto Nacional de Ecología, 2000). According to the fact that crocodylians are top predators, they occupy an important ecological role in their ecosystem. Culturally, they have been used for their meat and hides and are important in the cosmogony of ancient Mexican ethnic groups (Instituto Nacional de Ecología, 2000). Unfortunately, in Chiapas the crocodylians are facing several threats to their conser-

vation, *Crocodylus acutus* in particular is victim of poaching, mainly caused by the increase of human-crocodile conflicts and traffic, and is also threatened by habitat destruction (Thorbjarnarson et al., 2006; Sigler, 2010; Mandujano, 2011). *Crocodylus acutus* is vulnerable by the International Union for Conservation of Nature (Ponce-Campos et al., 2012) and subject to special protection in Mexico (Semarnat-2010). Nesting is one of the most critical periods of crocodylians life cycle (Cedillo-Leal et al., 2013) and it was estimated that up to 90% of *C. acutus* hatchlings die between hatching and the first year of age (Gaby et al., 1985; Thorbjarnarson, 1988; Mazzotti, 1989). Consequently, specific information about the parameters regulating this life cycle stage could improve survival rates and contribute to the conservation of the species. In Mexico, there have been studies on *C. acutus* nesting in Jalisco (Casas-Andreu, 2003; Valtierra-Azotla, 2007), Quintana Roo (Charruau et al., 2010; Charruau et al., 2011; Charruau, 2012; Charruau and Hénaut, 2012) and Oaxaca (Cedillo-Leal et al.,

1 - Centro de Investigación en Ciencias Biológicas Aplicadas, Universidad Autónoma del Estado de México, México

2 - Centro del Cambio Global y la Sustentabilidad en el Sureste A.C., Tabasco, México

*Corresponding author;

e-mail: tavomonroyvilchis@gmail.com

2013), and few description of nests were made in Nayarit (Hernández-Hurtado et al., 2011) and Jalisco (Cupul-Magaña et al., 2004). It has been mentioned that there is a latitudinal pattern, determined by temperature and precipitation, indicating that nesting begins earlier in lower latitudes (Thorbjarnarson, 1989; Casas-Andreu, 2003). In addition, it is documented that anthropogenic and some natural factors (Change in vegetation cover by hurricane) negatively affect nesting of *C. acutus* (Thorbjarnarson, 1996; Casas-Andreu, 2003; Thorbjarnarson et al., 2006; Charruau et al., 2010). However, very little information is known about the subject in Chiapas; still, some nesting data of *C. acutus* were reported in Sumidero Canyon National Park (Sigler, 2010). The objectives of this study are to determine key nesting characteristics of *C. acutus* in La Encrucijada Biosphere Reserve, Chiapas (Mexico) and to analyse environmental and anthropogenic factors that influence these characteristics.

Materials and methods

Study area

La Encrucijada Biosphere Reserve is on the coast of Chiapas, in the Pacific Coast Plain, between the 14°43' and 15°40' North and the 92°26' and 93°20' West; with a surface of 144 868 ha (Ine-Semarnap, 1999; fig. 1). The climate is Am (w), which means warm and humid with abundant rainfall in summer and a mean annual temperature of 28°C (Ine-Semarnap, 1999). This reserve has the only one Zapotonal forest (*Pachira aquatica*) in Mesoamerica and is also home of 309 species of plants, 54 species of fish with economic importance, 61 species of reptiles and amphibians, as well as 172 species of birds (Ine-Semarnap, 1999). In the reserve there is timber harvesting mangrove (*Rhizophora mangle*, *Avicennia germinans* and *Conocarpus erectus*), this causes deterioration in core areas (Tovilla-Hernández and Morales-García, 2013). In addition, in Chiapas there is a high incidence of intentional forest fires and agricultural practices (Román-Cuesta et al., 2013). Each year fires occur in the reserve and there is no systematic analysis of the damage on the flora and fauna.

Sampling and data collection

A 25.5 km survey was conducted daily from February to June 2014 on the “El Hueyate” estuary, on a boat 6 m long driven by a motor of 15 horsepower, nesting sites reviewed previous years (Sigler personal comments). Nesting areas

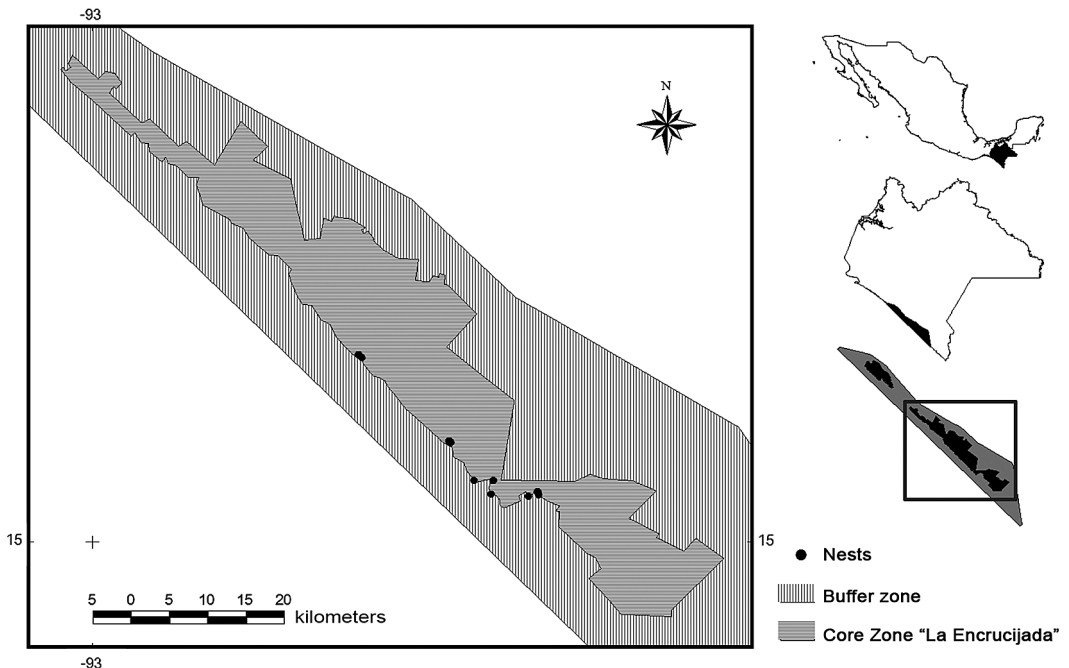


Figure 1. Location of La Encrucijada Biosphere Reserve and *Crocodylus acutus* nests. On the right, location of the Reserve within the contour of the Chiapas State (middle), and of Chiapas within Mexico (top).

and nests were identified by crocodile's tracks and georeferenced. Texture and soil type of nesting sites were obtained from the edaphology map (scale 1:250 000), available from the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO; <http://www.conabio.gob.mx/informacion/gis/>). The net primary productivity (NPP) was used as an indirect method to evaluate natural habitat resources available, which are susceptible to be used by consumers. This data was obtained from the global map of net primary productivity available from the portal of Global Land Cover Facility at resolution of 8 km (GLCF; <http://glcf.umd.edu/>).

The climatic factors measured were: a) air temperature under shade, b) air temperature at open sky, c) wind speed, d) burst of wind speed, e) relative humidity, f) atmospheric pressure, g) precipitation and h) solar radiation. Air temperature under shade (ATU) was recorded with a data logger (HOBO Pendant© Temperature/Alarm UA-001-08) located in the shade of a tree at 1.70 m of height and programmed to take measures every half hour during the incubation period. The others climatic factors were obtained from the automatic meteorological station La Encrucijada belonging to the Servicio Meteorológico Nacional de la Comisión Nacional del Agua (CONAGUA), Mexico. The station records the climatic factors every 10 minutes and the data were obtained from March 1th 2014 to May 30th 2014. To observe the variation of the climatic factors over nesting period, daily means were calculated.

The data evaluated for the nests were: distance to the closer tree (DCT), distance to the river (DR) and depth from the top of the nest to the first egg (DTF). Maximum length (MaL), minimum length (MiL) and depth were calculated for the incubation chamber (DIC). The measures were taken with a tape measure (± 0.5 mm). To determine the distance between the nest and the closest community, the trajectory was traced and measured by the river in Google Earth Pro 7.1.

The eggs were counted and extracted from each nest (NE); infertile (NIE) and broken eggs (NBE) were also considered. Every egg was weighed (WE), with a balance of 1000 g (± 1 g), and the maximum (MaLE) and minimum length (MiLE) were measured with a digital calliper (± 0.1 mm). At hatching, nests were revisited to count the number of hatched eggs (NHE), determine the hatching success (HS), nesting success and length of the incubation period (IP). For poached nests, they were interviewed local fishermen, about using American crocodile eggs to determine the causes of the destruction of nests.

Incubation temperature (IT) was recorded every half hour in seven nests with data loggers (HOBO Pendant© Temperature/Alarm UA-001-08). Data loggers were located at the half of the incubation chamber from the day of nest encounter and were removed off after hatching. With these data, incubation temperature was calculated during the thermosensitive period (TSP), which is the critical period of incubation where the temperature influences the gonadal differentiation for reptiles presenting a temperature-dependent sex determination (TSD) like crocodiles (Deeming, 2004). According to Aguilar-Miguel (1994) and Charruau (2012), *C. acutus* presents a female-male-female TSD pattern, with

the production of a majority of females at incubation temperatures $\leq 31^\circ\text{C}$ and $\geq 34^\circ\text{C}$ and the production of a majority of males at intermediate temperatures (i.e., $31.3\text{--}32^\circ\text{C}$). Possible pivotal temperature (PT, producing 50% of each sex) suggested by these studies are 31°C and 32.5°C .

Data analysis

The Spearman correlation was realized between the HS, IP and nests extern (DCT, DR and DTF) and intern characteristics (MaL, MiL and DIC). An ANOVA and a Pearson correlation test were used to assess differences of WE, MaLE and MiLE between nests. The egg weight average, clutch size and date of the beginning of the nesting season were reviewed from scientific notes from other localities along *C. acutus* distribution to perform simple regressions among these characteristics and the NPP, also among these characteristics and the latitude. An ANOVA was also realized to assess the difference of IT between nests and nesting months and a Spearman correlation was performed between the IT and nests characteristics. Every correlation was realized using the averages and standard deviations. A Student *t* test was performed to assess the differences between IT and ATU. Another ANOVA was realized to evaluate differences between temperatures of the TSP of each nest considering the period between days 25 and 45 of incubation as suggested by Charruau (2012), and a Student *t* test was realized to compare incubation temperature and the temperature of the nests during the estimated TSP. To evaluate the effects of climatic factors over the incubation temperature, multiple regressions were performed and three nest model types were built: (I) general model including every climatic factors evaluated, (II) model including factors that are affecting the most the variability percentage and (III) simplified model including factors with the best statistical significance ($p < 0.05$). These three models were based on the adjusted variability rate, which is the most appropriate for models including different variables. Finally, a Student *t* test was performed to compare distances with the closest community, and compare DCT and DR between hatched and poached nests a *U* Mann-Whitney test was realized.

Results

One hundred twenty-four surveys were realized and 34 nests were found in nine nesting areas (fig. 1), considering the definition of a nesting area suggested by Charruau et al. (2010). Seventeen nests were poached, 15 hatched and two were depredated, and all of them were located in the core area of the reserve. The laying period lasted 22 days (from March 2th to March 22th) as well as the hatching period (from May 14th to June 10th). The mean incubating period

was 74.6 ± 3.5 days ($n = 11$). The mean air temperature under shade was $28.52 \pm 3.05^\circ\text{C}$ and the mean relative humidity was $80.28 \pm 14.64\%$, decreasing in April and increasing in May. Precipitations recorded during the nesting period vary from 0 to 12.6 mm, reaching their highest in May (table 1). Nests in which incubation temperature was evaluated were in a range of 12 to 164 m from the meteorological station. Dominant soil type in nesting sites were Eutric Regosols and Glevico Solonchak, presenting medium and coarse texture, which means sandy ($n = 10$), sandy-loam ($n = 14$) and sandy-clay ($n = 10$).

The distance between the nest and the closest tree varied between 1.11 and 11.5 m, the mean distance to the river was 7.08 ± 5.76 m. Hatching success was 82.80% and nesting success was 30.36%. Eggs weights were between

80 and 140 g, with a maximum length between 66.6 and 89.2 mm (table 1). In general, poached nests were closer from a community (2.8 ± 1.19 km, range: 1.3-4.6 km) than hatching nests (6.9 ± 2.70 km, range: 1.8-8.6 km) ($t_{30} = 5.69$; $p < 0.001$).

Incubation temperatures were between 24.3 and 36.5°C (fig. 2), while in TSP were between 29.5 and 35.7°C . Based on results of Charrau (2012), four nests' temperatures favour females' production (34.69 , 33.24 , 29.97 and 34.04°C), two favoured the production of both sexes (32.47 and 31.16°C) and one favoured the production of a majority of males (31.46°C).

There was significant positive correlation between the distance from the nest to the river and the incubation time ($r = 0.64$, $p < 0.05$), which indicates the greater the distance from the

Table 1. Characteristics of the eggs and nests of *Crocodylus acutus* in La Encrucijada.

	Mean	SD	Range	<i>n</i>
Nests' extern characteristics				
Distance from the nest to the closest tree (m)	3.56	2.22	1.1-11.5	34
Distance from the nest to the river (m)	7.08	5.76	1.2-34.1	34
Depth from the top of the nest to the first egg (cm)	23	5.77	10.9-31.4	15
Air temperature under shade ($^\circ\text{C}$)	28.52	3.05	21.5-38.4	4048
Distance from the nest to the closest community (km)	5	2.94	1.3-8.6	34
Wind speed (km/h)	8.26	7.66	0-34.5	13 087
Relative humidity (%)	80.28	14.64	12-100	13 087
Precipitations (mm)	0.01	0.28	0-12.6	13 075
Atmospheric pressure (mmHg)	1009.81	1.86	910.4-1015	13 087
Solar radiation ($\text{W}\cdot\text{m}^2$)	216.52	320.09	0-1109	13 087
Burst of wind speed (km/h)	19.47	15.81	0-111.2	13 087
Air temperature ($^\circ\text{C}$)	27.90	3.40	20.4-37.8	13 087
Nests' intern characteristics				
Egg chamber maximum length (cm)	35.78	5.69	21.7-45	15
Egg chamber minimum length (cm)	29.71	4.4	18.4-36.1	15
Egg chamber depth (cm)	22.48	6.94	15.1-39.1	15
Incubation temperature ($^\circ\text{C}$)	32.10	1.68	24.3-36.5	7
Clutches characteristics				
Egg's weight (g)	104.58	9.98	80-140	426
Egg's maximum length (mm)	77.09	3.72	66.6-89.2	426
Egg's minimum length (mm)	47.88	1.58	42.2-52.5	426
Clutch size	34.28	6.74	22-44	14
Number of infertile eggs	3.5	2.13	0-7	14
Number of broken eggs	2	1.41	0-5	14
Number of hatched eggs	29.27	7.21	17-36	11
Nesting success (%)	30.36	40.96	0-94.44	30
Hatching success (%)	82.80	9.42	65.3-94.4	11
Incubation time (days)	74.63	3.5	70-82	11

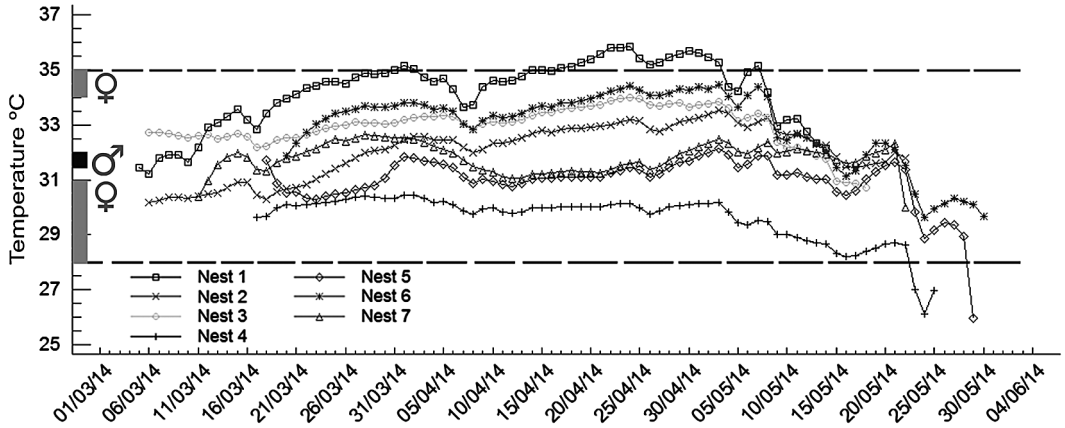


Figure 2. Incubation temperature of seven nests of *Crocodylus acutus* in la Encrucijada Biosphere Reserve. Dashed lines indicate the limits of lethal temperature of embryo.

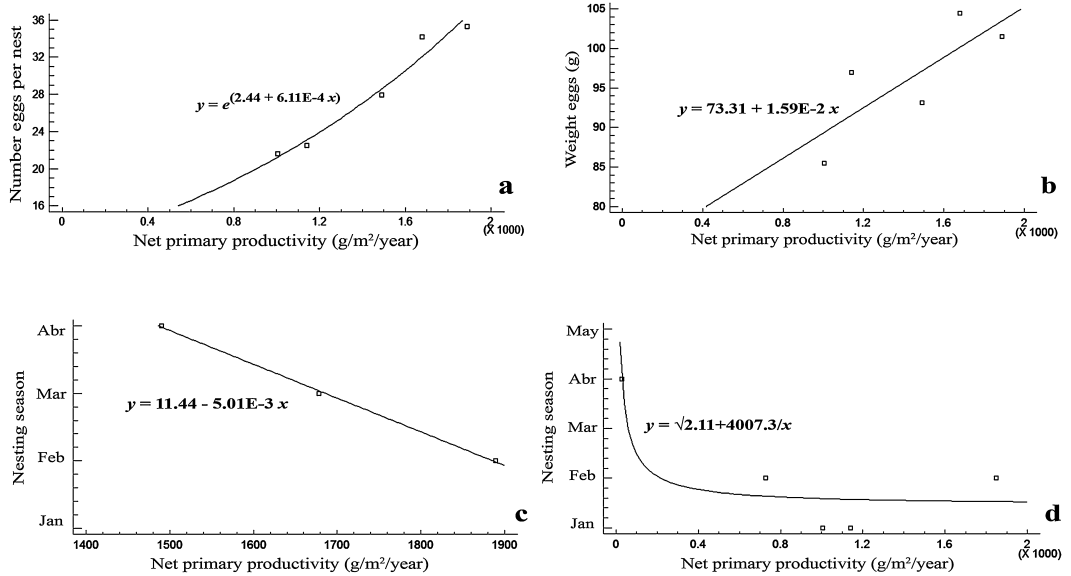


Figure 3. Regression models between the net primary productivity and some attributes of the clutches: (a) number of eggs ($r = 0.98$, $p < 0.05$) and (b) egg weight ($r = 0.81$, $p > 0.05$), and between the net primary production and the beginning of nesting: (c) Pacific slope ($r = -0.99$, $p < 0.05$) and (d) Gulf of Mexico and Caribbean region ($r = 0.97$, $p < 0.05$). The localities and values used for the regression models are showed in table 2.

nest to the river, the longer the incubation period. Analysis between HS, IP and nests' characteristics did not reveal a statistically significant relation. Differences between nests were found for the WE ($F_{13,412} = 205.21$; $p < 0.001$), MaLE ($F_{13,412} = 47.53$; $p < 0.001$) and MiLE ($F_{13,412} = 95.23$; $p < 0.001$).

There is a relation among the number of eggs and the PPN ($r = 0.98$, $p < 0.05$; fig. 3a),

the relation among the egg weight and the PPN is not significant, although a trend is notorious ($r = 0.81$, $p > 0.05$; fig. 3b). There is also a relation between PPN and the beginning of the nesting season, both for the Pacific slope ($r = -0.99$, $p < 0.05$; fig. 3c) as for the Gulf of México and the Caribbean ($r = 0.97$, $p < 0.05$; fig. 3d). These data show that nesting is earlier in places with bigger PPN; it is noteworthy that

Table 2. Beginning of the nesting season for *Crocodylus acutus* in different places of its distribution and some attributes of the clutches (WE: egg weight, NE: number of eggs per nest) that were related with the net primary productivity (NPP = $\text{g/m}^2/\text{year}$; fig. 3).

Locality	Nesting season	WE	NE	NPP	Author
Chiapas, Mexico	Mar	104.5	34.2	1678.15	This study
Panama	Jan-Feb	97.1	25.2	–	Balaguera-Reyna et al. (2015)
Oaxaca, Mexico	Feb-Mar	101.5	35.3	1889.14	Cedillo-Leal et al. (2013)
Q. Roo, Mexico	May-Jun	80	16.2	–	Charruau (2010)
Jalisco, Mexico	Apr-May	93.1	27.9	1490.52	Casas-Andreu (2003)
Dominican Republic	Jan-Mar	85.5	21.6	1004.50	Schubert (2002)
Cuba	Feb-Mar	–	–	1849.5	Alonso-Tabet et al. (2000)
Belize	Mar-May	85.6	22.3	–	Platt and Thorbjarnarson (2000)
Florida, USA	Apr-May	–	–	29.33	Thorbjarnarson (1989)
Haiti	Jan-Mar	97	22.5	1141.23	Thorbjarnarson (1989)
Panama	Feb-Mar	–	–	728.5	Dugan et al. (1981)

for these analyses, we only included references that show the specific location of the nests (table 2). The relation among the latitude and the beginning of the nesting season in the Pacific slope ($r = 0.90$, $p > 0.05$) and the Gulf of Mexico and the Caribbean region ($r = 0.30$, $p > 0.05$) are not significant.

The incubation temperatures were obtained for 73.8 days on average with data recorders. Incubation temperatures were significantly different between nests ($F_{6,24141} = 8037.92$; $p < 0.001$) and months ($F_{2,24145} = 729.89$; $p < 0.001$), reaching the highest temperature in April and the lowest in May. Incubation temperature presents a significant negative relation with the hatching success and the egg chamber depth ($r = -0.82$, $p < 0.05$ and $r = -0.85$, $p < 0.05$, respectively). Correlations realized with standard deviation were not statistically significant. ATU was significantly different from IT ($t_{28194} = 1.7767$; $p < 0.001$), with an average of 3.5°C . Both temperatures reached their highest in April. The mean temperature during the estimated TSP was significantly different between nests ($F_{6,7049} = 21396.59$; $p < 0.001$). The IT and the temperature of the TSP did not show statistical differences ($t_{12} = -0.43$; $p > 0.05$).

The climatic factors with influence in the incubation temperature were air temperature under shade, air temperature at open sky and solar radiation (table 3). Adjusted coefficient of

determination (adjusted R squared) is different between nests and models. The model I explain from 30.16 to 61.08%, the model II from 23.65 to 62.48% and the model III from 20.73 to 62.48% of the incubation temperature.

The DCT and DR between poached and hatched nests also present statistical difference ($U = 67.5$, $p < 0.05$ and $U = 51$, $p < 0.05$, respectively) and poached nests were found closer from a tree (3.14 ± 2.39 m) and from the river (4.60 ± 2.5 m) than hatched nests (4.25 ± 1.99 m and 9.72 ± 7.47 m, respectively). Finally, poached nests were significantly closer to a community than hatched nests ($t_{30} = 5.69$; $p < 0.001$).

Discussion

It has been described that the beginning of the American crocodile nesting season follows a latitude pattern that goes from the south to the north (Thorbjarnarson, 1989; Casas-Andreu, 2003). Our results do not support this hypothesis and with the information we have now, we show that there is no significant relation between latitude and the beginning of the nesting season (Pacific slope: $r = 0.90$, $p > 0.05$; Gulf of Mexico and Caribbean region: $r = 0.30$, $p > 0.05$). Although, our results suggest the beginning of the nesting season is due to the available natural resources in the nesting areas that could

Table 3. Variability percentage of the three models, with climatic factors included in the models I and II, and for the model III its coefficients. A: air temperature under shade, B: wind speed, C: burst of wind speed, D: air temperature at sun, E: relative humidity, F: atmospheric pressure, G: precipitations and H: solar radiation.

	Nest 1	Nest 2	Nest 3	Nest 4	Nest 5	Nest 6	Nest 7
Model I	ABCD	ABCD	ABCD	ABCD	ABCD	ABCD	ABCD
	EFGH	EFGH	EFGH	EFGH	EFGH	EFGH	EFGH
r^2	65.66	45.2	37.92	41.04	49.35	29.43	61.11
Adjusted r^2	61.08	38.75	30.16	33.67	42.71	20.61	56.17
Model II	ACH	ABCDE	ABCE	ADEFH	ABCDH	ABFG	ACFH
r^2	64.14	44.96	37.2	40.28	48.67	27.89	60.52
Adjusted r^2	62.48	41.08	33.51	34.85	43.78	23.65	58.16
Model III	ACH	ABD	A	DEFG	ADH	AG	ACH
r^2	64.14	42.62	32.05	35.85	44.73	22.93	58.99
Adjusted r^2	62.48	40.26	31.09	32.08	42.22	20.73	57.18
F	38.75	18.07	33.49	9.5	17.81	10.42	32.6
GI	3, 65	3, 73	1, 71	4, 68	3, 66	2, 70	3, 68
p -value	0	0	0	0	0	0	0
Constant	-1.062	6.887	17.455	-180.248	17.404	19.958	3.043
A	1.224	0.496	0.541	-	0.758	0.386	1.058
B	-	-0.248	-	-	-	-	-
C	-0.084	-	-	-	-	-	-0.086
D	-	0.465	-	0.281	-0.387	-	-
E	-	-	-	0.032	-	-	-
F	-	-	-	0.199	-	-	-
G	-	-	-	-3.47	-	-3.612	-
H	0.008	-	-	-	0.005	-	0.006

be used by the nesting females, measured indirectly by the terrestrial net primary productivity, this was observed for the Pacific slope (fig. 3c) and for the Gulf of Mexico and Caribbean region (fig. 3d). Intern and extern characteristics of *C. acutus*' nests in Mexico where evaluated at different locations (Casas-Andreu, 2003; Cupul-Magaña et al., 2004; Charruau et al., 2010; Sigler, 2010; Hernández-Hurtado et al., 2011; Cedillo-Leal et al., 2013) but there is not literature that evaluates those characteristics and their effect on hatching success. The results indicate that there is no relation between hatching success and extern and intern characteristics of the nest. However, it is necessary to assess several nesting periods because variations of nests characteristics and hatching success were found after abundant rainfall (Charruau et al., 2010).

The characteristics of the eggs found at La Encrucijada are among the highest values currently known for *C. acutus*, which indicates that females are middle-aged (Ferguson, 1985) and

likely reach large size (Thorbjarnarson, 1996). However, along the transect where nesting sites were found, less than five individuals presenting a total length over 2.41 m were captured and less than 15 individuals present a total length between 1.21 and 2.40 (Peña, 2011; most recent report on *C. acutus*' size in the zone), consequently, smaller clutches and lighter eggs would have been expected. It has been mentioned that there is a relationship between the weight and number of crocodilian eggs with female size (Thorbjarnarson, 1996). But our results also show that the characteristics of the eggs have a relationship with the NPP, i.e. at sites more productive females have more eggs (fig. 3a) and these have a greater weight (fig. 3b), with respect to females encountered in less productive sites. Further studies are needed to assess the reproductive effort to understand the above relationships. It is known for *C. acutus* that the temperature, precipitation, metabolic heat and

solar radiation influence the incubation temperature, and solar radiation is the most important heat source to maintain the temperature for the embryonic development (Charruau, 2012). Thus, climatic factors (macroclimate), nesting sites (mesoclimate) and processes occurring in the nest (microclimate) will determine incubation temperature and its fluctuations (Escobedo-Galván, 2012). The results indicate that the macroclimate and mesoclimate together will regulate, maintain, increase or decrease this temperature. We observed that every nest is affected by different factors but air temperature, solar radiation and air temperature under shade are the main factors influencing nest temperature, even if every factor that we analysed has a certain effect. Incubation temperatures (29.6-34.2°C) are similar to the one reported by Charruau (2012; 29.8-33.1°C) and are in the optimal range for embryonic development (Lang and Andrews, 1994). Georges et al. (2004) mentioned that the mean incubation temperature is not the good way to predict clutches' sexual proportion since it does not coincide with the mean temperature of the TSP; however, this study did not show significant differences.

These temperatures seem to permit the production of both sexes, but to favour females. In addition, to considerate the variation temperature promoting a specific sex, these variations have to be analysed (Neuwald and Valenzuela, 2011). Actually, temperatures recorded in this study suggest the production of both sexes; nevertheless, more research including hatchlings' sexing, would be necessary to understand that relation.

The incubation period depends on the temperature; low temperatures extend incubation time (Thorbjarnarson, 1989; Charruau, 2010). In this study, we did not have this tendency, but the incubation time showed a positive relation with the distance to the closest water source. Indeed, the closer the nest to the water, the shorter the incubation period. Distance from the nest to the water, influence nest temperature in the marine turtle *Caretta caretta*, farther nests having

higher temperature (Kasha et al., 2006). However, in this case nests being farther from the river should hatch before nests closer to the river, which is contrary to our results. Furthermore, there was no relation between mean nests temperature and distance to the river. Although, no explanation of this result has been found the gradient of soil humidity could be a factor involved. A certain degree of desiccation decreases fat exchanges and embryonic development (Staton and Dixon, 1977; Mazzotti et al., 1988). Nesting period occurs in dry season, the only source of humidity available comes from the estuary, and it is likely that nest closer to the river present higher humidity than remote nests.

In the reserve, people of local communities, the low availability of safe nesting sites and genetic and demographic factors (Peña, 2011) negatively affect *C. acutus*' populations. The present study showed that nest poaching and predation also affect *C. acutus* in the reserve because 56% of nests were lost for this reason; poaching being the most important threat toward nests (50% of the nests were affected). However, this factor has never been analysed in Mexico and we are trying to understand this problem in the study area. Poached nests were located closer to a tree and/or the river or any human community than hatched nests. Nests located closer from a tree and/or the river are more susceptible to poaching because traces left by the females during nest building are clearly apparent for people using the river as mean of transportation or using trees for their shade. Every area where nests were poached show evidence of human activity (e.g., empty bottles and food wastes).

During conversations with eight fishermen from the region, they mentioned that nest poaching was practiced for two reasons: eggs consumption and destruction. According to a popular belief, fresh crocodile's eggs would give a better sexual vitality and for this reason there is a strong demand, occasionally nests are poached for personal consumption or traffic. Eggs destruction is also done due to

fear of crocodiles and because they eat the same fish species as local communities. Fear for crocodiles is by the increasing number of human-crocodile conflicts in the area. Although there are reports of crocodile egg consumption in Mexico (Cifuentes and Cupul, 2004), there are no data on the number of poached nests and destroyed directly by anthropogenic activities. Whereas 50% of nests are pillaged, our results suggest that 578 eggs are lost nesting season. Egg consumption in wild nests by human of *Crocodylus intermedius* not allow the recovery of wild populations in Colombia and Venezuela (Castro et al., 2013). In addition to the above, in La Encrucijada other factors causing the decline of populations of crocodilians are the destruction of mangroves and swamps, drainage of ponds, forest fires and direct hunting (Aguilar-Galindo, 2005).

Even if *C. acutus*' perspective is unfavourable in the study area, 12 nests hatched in a zone where there is flora and fauna conservation plans (Concepcion Island). Up to date, this is the safest nesting site for *C. acutus* in the reserve; this coincides with observations made in Lagunas de Chachahua National Park, Oaxaca (J. García-Grajales pers. com.) where community participation has been the linchpin for the monitoring and conservation of *C. acutus*.

In conclusion, there is a positive and significant relationship between primary production and the start of the nesting season for the Pacific coast, and the Gulf of Mexico and the Caribbean. Nests were built in uplands and external and internal nests characteristics are similar to reports from other sites. Clutch characteristics (i.e., weight and egg dimensions) seem to be determined by nesting sites' resources availability along with females' age and size. Temperature and time incubation are in relation with nests characteristics and temperature of the studied year seem to favour female production. However, it is necessary to include hatchlings' sexing in future studies and compare sexual proportion with incubation temperatures. Climatic factors have an impact on incubation

temperature and, consequently, it is important to keep monitoring crocodile nests in order to know female adaptation strategies in response to weather variations. In La Encrucijada, *C. acutus* populations are affected by nest poaching for egg consumption, destruction and traffic. These reasons justify the importance of a short, medium and long term systematic monitoring of the area to observe the effect of poaching on the population dynamic. Promoting communities' participation is also important to change the attitude and perception towards crocodiles.

Acknowledgements. To Mexican people for funding through CONACYT, number 360827, and the Autonomous University of the State of Mexico (project 3841/2014 / CIA). To Crocodile Specialist Group-IUCN by the Student Research Assistance Scheme. The local people of the Island Conservation Project Conception, for lending their facilities for this work. To Luis Sigler and Didier Labarre for helping with the review and English translation.

References

- Aguilar-Galindo, A. (2005): Evaluación del estado de conservación del *Caiman crocodilus fuscus* (Mertens, 1943) durante el año 2003-2004, en el sistema lagunar de Chantuto, Reserva de la Biosfera La Encrucijada, Chiapas, México. Tesis de Licenciatura, Universidad Autónoma Metropolitana, Xochimilco, México.
- Aguilar-Miguel, X. (1994): Efecto de la Temperatura de Incubación Sobre la Determinación del Sexo en *Crocodylus acutus* y *C. moreletii*. Tesis de Maestría, Universidad Nacional Autónoma de México, México.
- Alonso-Tabet, M., Rodríguez-Soberón, R., Berovides-Álvarez, V., Hernández-Fuentes, C.E. (2000): Influencia de la geomorfología del hábitat sobre la nidificación de *Crocodylus acutus* en el refugio de fauna Monte Cabaniguán, Cuba. In: Crocodiles Proceedings of the 15th Working Meeting of the Crocodile Specialist Group, p. 42-58. IUCN The World Conservation Union, Gland, Switzerland and Cambridge, UK.
- Álvarez del Toro, M. (1974): Los Crocodylia de México (Estudio Comparativo). Instituto Mexicano de Recursos Naturales Renovables, A.C. México.
- Balaguera-Reyna, S.A., Venegas-Anaya, M., Imperio, O., Lessios, H.A., Densmore, L.D. (2015): Reproductive ecology and hatchling growth rates of the American crocodile (*Crocodylus acutus*) on Coiba Island, Panama. S. Amer. J. Herp. **10**: 10-22.
- Casas-Andreu, G. (2003): Ecología de la anidación de *Crocodylus acutus* (Reptilia: Crocodylidae) en la desembocadura del río Cuitzmala, Jalisco, México. Acta Zool. Mex. **89**: 111-128.

- Castro, A., Merchán, M., Garcés, M., Cárdenas, M., Gómez, F. (2013): Uso histórico y actual del caimán llanero (*Crocodylus intermedius*) en la Orinoquia (Colombia-Venezuela). *Biota Col.* **14**: 65-82.
- Cedillo-Leal, C., García-Grajales, J., Martínez-González, J.C., Briones-Encinia, F., Cienfuegos-Rivas, E. (2013): Aspectos ecológicos de la anidación de *Crocodylus acutus* (Reptilia: Crocodylidae) en dos localidades de la costa de Oaxaca, México. *Acta Zool. Mex.* **29**: 164-177.
- Charruau, P. (2010): Ecología y etología de anidación del cocodrilo americano (*Crocodylus acutus*): Un estudio para su conservación. Tesis de Doctorado, El Colegio de la Frontera Sur, Chetumal, Quintana Roo, México.
- Charruau, P. (2012): Microclimate of American crocodile nests in Banco Chinchorro biosphere reserve, Mexico: effect on incubation length, embryos survival and hatchlings sex. *J. Therm. Biol.* **37**: 6-14.
- Charruau, P., Hénaut, Y. (2012): Nest attendance and hatching care in wild American crocodiles (*Crocodylus acutus*) in Quintana Roo, Mexico. *Anim. Biol.* **62**: 29-51.
- Charruau, P., Thorbjarnarson, J.B., Hénaut, Y. (2010): Tropical cyclones and reproductive ecology of *Crocodylus acutus* Cuvier, 1807 (Reptilia: Crocodylia: Crocodylidae) on a Caribbean atoll in Mexico. *J. Nat. Hist.* **44**: 741-761.
- Charruau, P., Méndez-De La Cruz, F.R., González-Cortés, H. (2011): Preliminary results on nesting ecology of *Crocodylus acutus* on Cozumel Island, Mexico. *Croc. Spec. Group Newsl.* **30**: 29-32.
- Cifuentes, J.L., Cupul, F. (2004): ¿Los terribles cocodrilos? Secretaría de Educación Pública, Fondo de Cultura Económica y Consejo Nacional de Ciencia y Tecnología, México.
- Cupul-Magaña, F.G., Niz-Villaseñor, A., Reyes-Juárez, A., Rubio-Delgado, A. (2004): Historia natural del cocodrilo americano (*Crocodylus acutus*) en el estero Boca Negra, Jalisco, México: Anidación y crecimiento de neonatos. *Ciencia y Mar* **8**: 31-42.
- Deeming, D.C. (2004): Prevalence of TSD in crocodylians. In: *Temperature-Dependent Sex Determination in Vertebrates*, p. 33-41. Valenzuela, N., Lance, V.A., Eds, Smithsonian Institution, Washington.
- Dugan, B.A., Rand, A.S., Burghardt, G.M., Bock, B.C. (1981): Interactions between nesting crocodiles and iguanas. *J. Herpetol.* **15**: 409-414.
- Escobedo-Galván, A. (2012): Efecto del clima sobre la proporción de sexos del cocodrilo americano (*Crocodylus acutus*) y cocodrilo de pantano (*C. moreletii*) y posibles implicaciones ante el cambio climático. Tesis de Doctorado, Instituto de Ecología. Universidad Nacional Autónoma de México, México, DF.
- Ferguson, M.W.J. (1985): Reproductive biology and embryology of the crocodylians. In: *Wildlife Management: Crocodiles and Alligators*, p. 427-444. Gans, C., Billet, F., Maderson, P.F.A., Eds, Chipping Norton, Australia.
- Gaby, R., Macmahon, M.P., Mazzotti, F., Gillies, W.N., Wilcox, J.R. (1985): Ecology of a population of *Crocodylus acutus* at a power plant site in Florida. *J. Herpetol.* **19**: 189-198.
- Georges, A., Doody, S., Beggs, K., Young, J. (2004): Thermal models of TSD under laboratory and field conditions. In: *Temperature-Dependent Sex Determination in Vertebrates*, p. 79-89. Valenzuela, N., Lance, V., Eds, Smithsonian Institution Press, Washington, DC.
- Hernández-Hurtado, H., Romero-Villaruel, J.J., Hernández-Hurtado, P.S. (2011): Ecología poblacional de *Crocodylus acutus* en los sistemas estuarinos de San Blas, Nayarit, México. *Rev. Mex. de Biodivers.* **82**: 887-895.
- Instituto Nacional De Ecología, INE (2000): Proyecto para la conservación, manejo y aprovechamiento sustentable de los Crocodylia de México (COMACROM). Instituto Nacional de Ecología y Secretaría de Marina y Recursos Naturales, Distrito Federal, México.
- Instituto Nacional De Ecología-Secretaría De Medio Ambiente, Recursos Naturales Y Pesca, INE-SEMARNAP (1999): Programa de manejo Reserva de la Biosfera La Encrucijada, México. Instituto Nacional de Ecología. Secretaría de Medio Ambiente, Recursos Naturales y Pesca.
- Kasha, Y., Ilgaz, C., Özdemir, A., Baskale, E., Türkozan, O., Baran, I., Stachowitsch, M. (2006): Sex ratio estimations of loggerhead sea turtle hatchlings by histological examination and nest temperatures at Fethiye beach, Turkey. *Natway* **93**: 338-343.
- Lang, J.W., Andrews, H.V. (1994): Temperature-dependent sex determination in crocodylians. *J. Exp. Zool.* **270**: 28-44.
- Mandujano, H.M. (2011): Cultura y actitud hacia el cocodrilo (*Crocodylus acutus*) por usufructuarios del río Grijalva en Chiapas, México. *Quehacer Científico en Chiapas* **9**: 10-23.
- Mazzotti, F.J. (1989): Factors affecting the nesting success of the American crocodile, *Crocodylus acutus*, in Florida bay. *Bull. Mar. Sci.* **44**: 220-228.
- Mazzotti, F.J., Kushlan, J.A., Dunbar-Cooper, A. (1988): Desiccation and cryptic nest flooding as probable causes of egg mortality in the American crocodile, *Crocodylus acutus*, in Everglades National Park, Florida. *Fla. Sci.* **51**: 65-72.
- Neuwald, J.L., Valenzuela, N. (2001): The lesser known challenge of climate change: thermal variance and sex-reversal in vertebrates with temperature-dependent sex determination. *PLoS One* **6**: e18117.
- Peña, M.E.J. (2011): Abundancia relativa de *Crocodylus acutus* y *Caiman crocodilus* en la Reserva de la Biosfera La Encrucijada en Chiapas, México. Tesis de Licenciatura, Facultad de Medicina Veterinaria y Zootecnia, Universidad Autónoma de Chiapas, México.
- Ponce-Campos, P., Thorbjarnarson, J., Velasco, A. (2012): *Crocodylus acutus*. The IUCN Red List of Threatened Species. Version 2014.3. www.iucnredlist.com. Downloaded on 09 March 2015.
- Román-Cuesta, R.M., Retama, J., Gracia, M. (2013): Caracterización del régimen de incendios forestales en el trópico mexicano: el caso de Chiapas. In: *La biodiversidad en Chiapas: Estudios de Estado*, p. 337-349. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Eds, CONABIO – Gobierno del Estado de Chiapas, México.

- SEMARNAT, Secretaría de Medio Ambiente y Recursos Naturales (2010): Norma Oficial Mexicana NOM-059-SEMARNAT-2010. Diario Oficial de la Federación (DOF), jueves 30 de diciembre de 2010.
- Sigler, L. (2010): La historia natural del Cocodrilo Americano *Crocodylus acutus* en el Parque Nacional Cañón del Sumidero, Chiapas, México. *Rev. Lat. Cons.* **1**: 73-82.
- Staton, M.A., Dixon, J.R. (1977): Breeding biology of the spectacled caiman, *Caiman crocodilus crocodilus*, in the Venezuelan Llanos. Wildlife Research Report 5, Fish and Wildlife Service, USA.
- Thorbjarnarson, J.B. (1988): Status and ecology of American crocodile in Haiti. *Bull. Fla. State Mus.* **33**: 1-86.
- Thorbjarnarson, J.B. (1989): Ecology of the American crocodile, *Crocodylus acutus*. In: Crocodiles. Their Ecology, Management, and Conservation, p. 228-259. A special publication of the Crocodile Specialist Group. IUCN, Gland, Switzerland.
- Thorbjarnarson, J.B. (1996): Reproductive characteristics of the order Crocodylia. *Herpetologica* **52**: 8-24.
- Thorbjarnarson, J.B., Mazzotti, F., Sanderson, E., Buitrago, F., Lazcano, M., Minkowski, K., Muñoz, M., Ponce, P., Sigler, L., Soberón, R., Trelancia, A.M., Velasco, A. (2006): Regional habitat conservation priorities for the American crocodile. *Biol. Conserv.* **128**: 25-36.
- Tovilla-Hernández, C., Morales-García, B. (2013): Uso de la madera de mangle en comunidades de la Reserva La Encrucijada. In: La biodiversidad en Chiapas: Estudios de Estado, p. 238-240. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Eds, CONABIO – Gobierno del Estado de Chiapas, México.
- Uetz, P., Hošek, J., Eds (2014): The Reptile Database, <http://www.reptile-database.org>. Consultation: 22/10/2014.
- Valtierra-Azotla, A.M. (2007): Ecología poblacional y reproductiva del cocodrilo americano (*Crocodylus acutus*), en la Reserva de la Biosfera Chamela-Cuixmala. Tesis Maestría. Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México.

Submitted: February 8, 2016. Final revision received: May 17, 2016. Accepted: June 19, 2016.
Associate Editor: Luca Luiselli.