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# Using regression tree analysis to determine size class intervals and sexual dimorphism in the Morelet's crocodile *Crocodylus moreletii*

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Assignment of Morelet's crocodile *Crocodylus moreletii* individuals into size groups or classes based on ecological and morphological similarities has not yet been associated with species-specific ontogeny related changes. Age or size of first reproductive behavior is not precisely known for *C. moreletii*, but differences in allometric patterns and relative cranial size between juveniles and adults might be used as an indicator of sexual maturity. In this study, a regression tree analysis was used to investigate the relationship between age and body size in 1266 crocodiles by using both simple and generalized linear models, with gender and origin (captive or wild) as factors. Total length (TL), snout–vent length (SVL) and cranial length (CL) were used as predictor variables and the logarithm of body mass as the response variable. Four length intervals with well-defined thresholds (514, 899 and 1497 mm of TL) were established using all three predictors (TL, SVL and CL). Relationship between SVL and TL was described, and a strong positive relationship ( $r^2=0.98$ ), unaffected by crocodile gender, was observed. The observed CL–TL and CL–SVL relationships were also positive but significantly different between males and females ( $p < 0.001$ ) and length interval classes ( $p=0.01$ ). These results suggest that our estimated size thresholds seem to correspond to important ontogenetic changes in *C. moreletii* and that sexual maturity is closely related to size in this species, where sexual dimorphism in body length occurs, particularly in large individuals (size group IV).

Keywords: allometric patterns, Crocodylia, general linear models, sexual maturity, size group

Age in wild crocodylians is rarely known and so, body size measurements such as total length (TL) or snout–vent length (SVL) are often used as indicators of sexual maturity (i.e. juvenile or adult). Body size in crocodylians, and many other vertebrates, is known to better relate to major ontogenetic changes rather than age (Bluweiss et al. 1978, Wilkinson and Rhodes 1997, Platt et al. 2009). Some models have been proposed to estimate age from body size measurements in crocodiles (Charruau 2011, Suárez-Coya et al. 2013), but to have a better understanding of population dynamics, it would be useful to have an age/size classification based on a

morphological analysis that considers ontogenetic changes (Barrios-Quiróz et al. 2012).

Classification in size classes based on ecological and morphological similarities have been used for the Morelet's crocodile *Crocodylus moreletii* in several studies (Hunt 1977, Platt et al. 2006, 2009, Cedeño-Vázquez et al. 2011). These size classes are usually set within 50 cm increments, and this classification is useful to estimate crocodile size during spotlight surveying, by reducing the estimation error due to observer bias (Messel et al. 1981). However, this classification has also been used by some authors to assign development stages, where each class corresponds to an arbitrarily defined life stage category: class I 'hatchling' (TL  $\leq$  500 mm); class II 'juvenile' (500 mm  $<$  TL  $\leq$  1000 mm); class III 'sub-adult' (1000 mm  $<$  TL  $\leq$  1500 mm) and class IV 'adult' (TL  $>$  1500 mm); despite the fact that in *C. moreletii* many of the morphological and physiological changes associated with aging are still poorly understood (Platt et al.

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2009). For this reason, categories based on size classes could not yet be associated with ontogeny in this crocodile species, which biologically, does not make sense.

Age or size at sexual maturity (or first reproductive behavior) is not precisely known in *C. moreletii*, but changes in allometric patterns (i.e. regression slopes) between juveniles and adults are considered as secondary sexual traits in vertebrates (Emerson 2000) and can be used as an indicator of sexual maturity. For example, female common snapping turtles *Chelydra serpentina* have a decrease in longitudinal growth rate when they attain sexual maturity (assessed by ovarian follicle growth analysis; Christiansen and Burken 1979, Galbraith et al. 1989). Furthermore, longitudinal growth rate virtually stops when these female turtles initiate their first nesting behavior. Similar observations were reported for males of this species, where longitudinal growth rate decreases when they reach sexual maturity (assessed through the presence of motile spermatozoos in the epididymis; Christiansen and Burken 1979, Galbraith et al. 1989).

Some studies have reported reproductive female *C. moreletii* TL ranging from 1350 to 2190 mm (Hunt 1975, Casas-Andreu 1986, Platt et al. 2008, Casas-Andreu et al. 2011), and one in particular, reported a TL estimation of 1210 mm for a reproductive female based on observations between nest size and nesting female's TL (Platt et al. 2008). *Crocodylus moreletii*, like other crocodylian species exhibits sexual dimorphism (related to body size) with males usually exhibiting higher growth rates than females. However, *C. moreletii* females seem to attain sexual maturity more rapidly than males (Platt et al. 2009, Casas-Andreu et al. 2011, Barrios-Quiroz et al. 2012, Suárez-Coya et al. 2013).

Body length (TL or SVL) and head morphology in *C. moreletii* are variables that need to be considered when comparative analyses exploring the difference between males and females are to be performed, as cranial shape and relative size may be associated with ontogenetic changes in diet during growth (Barrios-Quiroz et al. 2012). As a crocodile grows, its ability to capture larger prey items also increases, with adult crocodiles being able to prey upon larger animals such as mammals and big fish (Platt et al. 2006, Wallace and Leslie 2008, Cedeño-Vázquez et al. 2014). Crocodile species that prey upon larger animals tend to usually have shorter and wider snouts (McHenry et al. 2006, Blanco et al. 2015). Based on that observation, we formulated the hypothesis that in *C. moreletii* the relationship slope observed between body length (TL or SVL) and cranial length (CL) in adults would be less than the one observed for previous size classes (hatchling, juvenile and sub-adult) due to dietary changes. Therefore, the main hypothesis explored in this study was that the inflection points in the allometric model between length (TL, SVL or CL) and body mass would be the average size at which *C. moreletii* reaches sexual maturity, recognizing then at least two size classes that correspond to relevant physiological changes in this species. Data from previous studies suggest that, overall, *C. moreletii* females are smaller than males and usually attain maximum sizes of between 2000 and 2500 mm (Barrios-Quiroz et al. 2012). On the other hand, in other crocodylian species, such as *Alligator mississippiensis* and *Caiman latirostris*, significant difference in the CL–TL relationship was observed between the two

sexes and sexual dimorphism in the allometric growth of the skull was reported (Woodward et al. 1995, Verdade 2000). As such, we have also hypothesized that the inflection points in our allometric model between length (TL, SVL or CL) and body mass would then also differ between sexes.

## Material and methods

*Crocodylus moreletii* morphological information used in this study was collected within the natural distribution of the species, from the state of Tamaulipas (northeast Mexico), through the coastal states in the Gulf of Mexico to the Yucatan Peninsula (Fig. 1). The morphometric dataset was compiled using information from previous published studies (Escobedo-Galván et al. 2009, Padilla et al. 2009, 2010, González-Jáuregui et al. 2012), crocodile farms and results of the *C. moreletii* national monitoring program in Mexico (CONABIO 2015). In this monitoring program, all crocodiles occurring in areas where the American crocodile *Crocodylus acutus* is also known to be present, were thoroughly inspected by experts and only individuals they considered as *C. moreletii*, based on morphological characteristics (Sánchez-Herrera et al. 2011), were added to the national program's database. Data from wild crocodiles in the Mexican state of Campeche were collected by SEP and MGJ, following the standardized protocol delineated in the national *C. moreletii* monitoring program in Mexico: crocodiles were located by their eyeshine when illuminated with a spotlight during nocturnal surveys conducted from an aluminum boat with a 15 HP motor and captured and manually restrained using an aluminum pole with a break-away stainless-steel noose (Sánchez-Herrera et al. 2011). Data collection on captive-reared crocodiles was conducted during regular daily activities in the farms. For both wild and captive-reared crocodiles, immediately after capture, body mass (W) was determined ( $\pm 0.1$  g accuracy in individuals less than 500 mm TL and  $\pm 10$  g in larger individuals) and three measures of length were taken using a measuring tape (accuracy  $\pm 1$  mm): I) cranial length (CL), measured along the dorsal surface starting on the anterior tip of the snout to the median posterior edge of the supraoccipital bone (Fig. 2A); II) total length (TL), measured along the ventral surface starting on the tip of the snout to the end of the tail (Fig. 2B); III) snout–vent length (SVL), measured along the ventral surface starting from the tip of the snout until the anterior margin of the cloaca. Sex was determined by direct examination of the cloaca (Ziegler and Olbort 2007) and sex ratio was tested against the null hypothesis of a 1:1 with a  $\chi^2$ -test (Cedeño-Vázquez et al. 2006). All crocodiles were marked by either the removal of a unique combination of three vertical tail scutes (Platt et al. 2009, Sánchez-Herrera et al. 2011) or by attaching a numbered metal tag to the interdigital membrane in both rear feet (Sánchez-Herrera et al. 2011).

Allometric relationships were assessed by performing an analysis of covariance (simple linear model approach; Rutherford 2011) and a comparison between sexes was performed through three models: model 1 – SVL was specified as the response variable and TL as the covariable; model 2 – CL was defined as the response variable and TL the covariable;

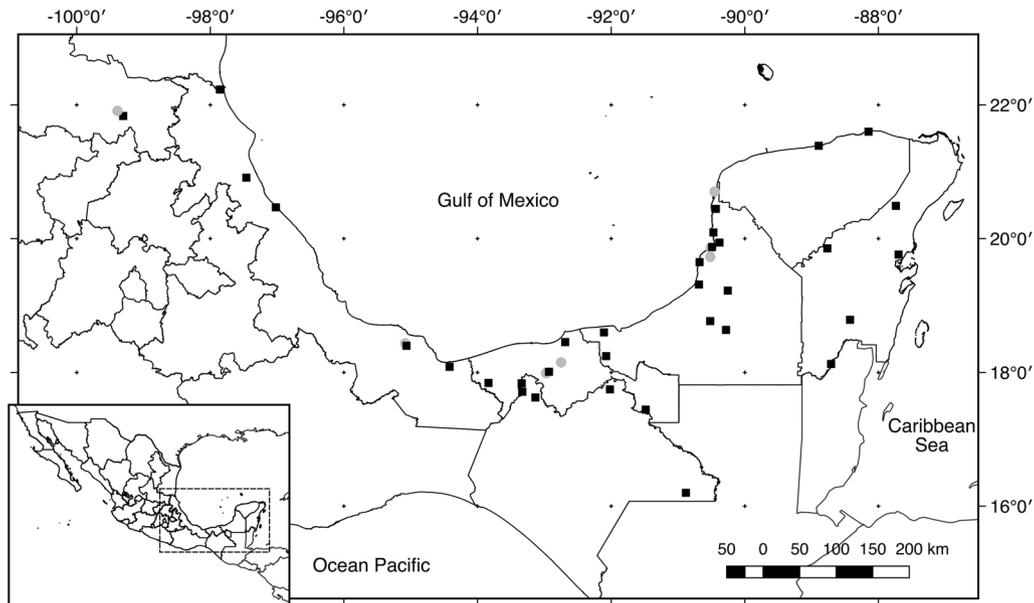


Figure 1. Sample sites of *Crocodylus moreletii* used in this study. Gray and black dots indicate, respectively, captive-reared and wild crocodiles.

model 3 – CL was specified as the response variable and SVL as the covariable.

Regression trees to determine crocodile size groups were performed as they are a robust method for exploring and describing patterns between a response variable and multiple predictor variables (Debeljak and Džeroski 2011). Regression tree models were created through a process of recursive division of data into two subsets. For each predictor variable the modelling process iteratively determines the best data split value (branch node) that minimizes the sum of squared deviations from the split response means. The predictor variable (and estimated node) with the smallest deviation is then considered as the first division in the tree (upper split) and it can be interpreted as the best explanation for the variation observed in the response variable. From this initial node, two branches then descend representing two subsets

of data, where the left branch symbolizes ‘less than’ (<) and the right branch symbolizes ‘greater than’ (>) the threshold value (node) in the predictor variable. This partitioning process then continues recursively for each branch until a specific number of branches has been produced or a predefined minimum number of observations within the branch has been obtained (Logan 2010, Debeljak and Džeroski 2011).

The natural logarithm of body mass was defined as the response variable in the regression tree, and a length measure (CL, TL or SVL), sex (male or female) and origin (wild or captive) as predictor variables. Regression tree analysis was then performed using each length measure (TL, SVL, CL) separately. The predicted threshold values from the resulting regression tree models were compared to the values used by previous studies to classify individuals of *C. moreletii* in size classes of TL (Escobedo-Galván et al. 2009, Padilla et al.

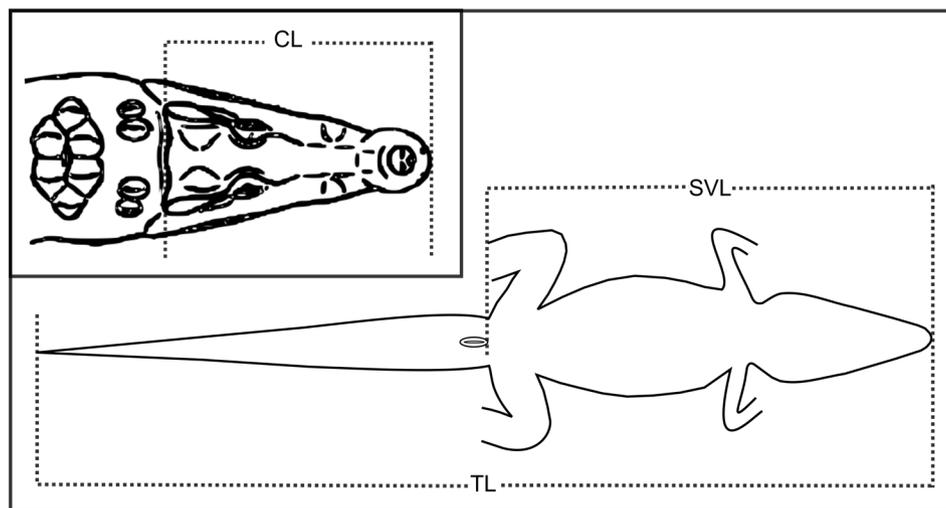


Figure 2. Crocodile length measurements used in this study (cranial length – CL; total length – TL; snout–vent length – SVL). TL and SVL measurements were taken along the ventral surface, while CL was measured on the dorsal side.

Table 1. Descriptive values (sample size, mean and minimum–maximum) of wild and captive-reared *C. moreletii* morphometric measurements (total length, snout–vent length, cranial length and body mass) captive and wild used in this study. All measurements are in millimeters (mm) with the exception of body mass, which is in grams (g).

	Sex		All
	Males	Females	
Sample size (n)	545	486	1031 + 235 no determined (1.2:1 sex ratio)
Captive	101	170	204 no determined
Wild	444	316	31 no determined
Total length (TL)	1021 (240–3110)	1129 (254–2623)	1004 (218–3110)
Captive	1692 (366–2880)	1591 (358–2350)	
Wild	881 (254–2623)	869 (240–3110)	
Snout–vent length (SVL)	506 (101–1672)	565 (120–1360)	498 (101–1672)
Captive	878 (180–1600)	808 (170–1300)	
Wild	427 (101–1672)	438 (120–1360)	
Cranial length (CL)	139 (31–470)	163 (40–360)	141 (31–470)
Captive	245 (46–400)	254 (57–330)	
Wild	124 (31–470)	129 (40–360)	
Body mass (W)	12 675 (30–150 200)	12 034 (40–80 200)	10 281 (27–150 200)
Captive	43 763 (200–150 200)	25 157 (510–80 200)	
Wild	6416 (30–140 000)	5410 (40–75 000)	

2009, 2010, González-Jáuregui et al. 2012), where each class corresponds to an arbitrarily defined category.

Generalized linear models (GLM) with a gamma distribution and natural log link to fit the response variable (body mass) were used to compare the relationship slopes between TL–W, SVL–W and CL–W, within each length interval group determined by the thresholds estimated through regression trees and sex (male or female). Another GLM (Gamma family, log function link), using CL as the response variable, sex and regression tree length interval groups as factors and TL as a covariable, was then used to identify any CL–TL differences amongst length classes. In all models, statistical significance was established at  $\alpha < 0.05$ . All analyses described above were performed using the software packages r-part (Therneau et al. 2019) and gmodels (Warnes et al. 2018) for R statistical software (<www.r-project.org>).

## Results

The morphometric dataset used in this study contained information from a total of 1266 *Crocodylus moreletii* individuals, of which 475 (38%) had captive-reared origin and 791 (62%) were free-ranging animals. From the total number of individuals, 486 crocodiles were identified as females, 545 as males and 240 crocodiles were unable to confidently determine gender through cloacal inspection due to their small body size (TL < 500 mm). Observed sex ratio was 1.2:1 (male:female) and did not differ from the theoretically expected 1:1 ( $\chi^2 = 3.3763$ ,  $df = 1$ ,  $p > 0.05$ ), which indicated an overall well representation of both sexes in the analyses. In males, mean TL and SVL was 1021 mm and 506 mm, respectively, whereas for females the values were 1129 mm and 565 mm. Mean CL value for males and females was, respectively, 139 mm and 141 mm (Table 1).

Snout–vent length exhibited a positive relation with TL for both males (SVL =  $0.51 \times TL - 12.498$ ;  $r^2 = 0.99$ ) and females (SVL =  $0.515 \times TL - 15.74$ ;  $r^2 = 0.98$ ), without significant difference between sexes being observed ( $F_{1,1016} = 2.93$ ;  $p = 0.08$ ). CL was positively related with TL

for both males (TL =  $0.137 \times CL + 8.131$ ;  $r^2 = 0.98$ ) and females (TL =  $0.142 \times CL + 5.95$ ), also without significant difference between sexes being observed ( $F_{1,899} = 25.74$ ;  $p < 0.001$ ). Similar results were observed in the relationship between CL and SVL (Fig. 3) for both males (SVL =  $0.268 \times CL + 11.768$ ;  $r^2 = 0.98$ ) and females (TL =  $0.274 \times CL - 11.12$ ;  $r^2 = 0.98$ ), without significant difference between sexes being observed ( $F_{1,899} = 8.35$ ;  $p < 0.01$ ; Fig. 3).

Regression tree analysis using a measure of length (TL, SVL or CL), sex and crocodile origin (captive or wild) as predictors and the natural logarithm of body mass as response variable outputted three threshold values which resulted in the identification of four length class intervals. Thresholds values when using TL as measure of length were estimated at 514, 891 and 1499 mm (Table 2, Fig. 4A), with approximately 75% of variation observed in body mass being explained by TL (crocodile origin and sex explained 14% and 11%, respectively). Similar results were observed in the regression tree analysis using SVL, which also estimated three threshold values (239, 434 and 746 mm) separating four length class intervals (Table 2, Fig. 4B), with approximately 75% of variation observed in body mass being explained by SVL (crocodile origin and sex explained 10% and 15%, respectively). When using CL as the measure of length, three threshold values were also identified (81, 135 and 213 mm; Table 2, Fig. 4C), with CL accounting for 86% of variation in body mass, and sex and crocodile origin explaining 5% and 9%, respectively.

GLM analyses indicated significant differences in the crocodile size (TL, SVL, CL) – body mass relationships between length class intervals (except between group I and II) identified in the regression tree analyses. No significant difference was observed between males and females in all three models (Fig. 5).

Significant difference was observed in the TL–CL relationship ( $F_{1,887} = 21.01$ ,  $p < 0.001$ ) between males and females and amongst identified length class intervals ( $F_{3,893} = 4.20$ ,  $p < 0.01$ ). No significant difference was observed in the sex–length class intervals interaction ( $F_{3,887} = 0.677$ ,  $p = 0.56$ ; Fig. 6).

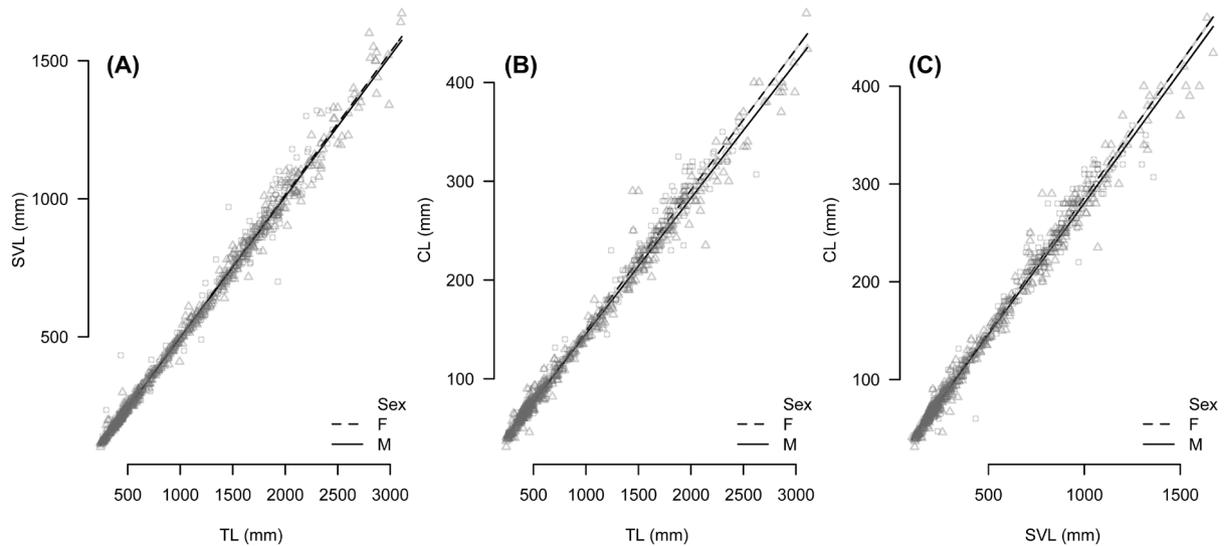


Figure 3. Crocodile total length (TL), snout-vent length (SVL) and cranial length (CL) dispersion and regression line relationships by sex (triangles = males; circles = females). (A) TL–SVL; (B) TL–CL; (C) SVL–CL. All lengths are expressed in millimeters.

## Discussion

Our study aimed to identify intervals of crocodile size (length class) that are most likely to correspond to different life stages of *Crocodylus moreletii*, based on morphometric data from both wild and captive-reared individuals across the species distribution range in Mexico. Overall, four length classes were identified by the regression tree models (RTM) and observed intervals exhibited similar threshold values to the ones previously used in *C. moreletii* studies involving the use of arbitrarily defined size classes based on ecological and morphological similarities (Platt et al. 2006, 2009, Cedeño-Vázquez et al. 2011, Sánchez-Herrera et al. 2011). Highest difference in threshold transition values between our RTM results and previous literature was observed (110 mm; Table 3) between length class II (juvenile) and III (sub-adult). Threshold transition values for length classes I (hatchling) – II (juvenile) and III (sub-adult) – IV (adult) was, respectively, 0.1 mm and 0.3 mm, which was deemed insignificant.

Sex ratio observed in our study was balanced (minimum deviation from 1:1) and similar to what has been previously reported for wild *C. moreletii* (1:1.3 in Cedeño-Vázquez et al. 2006, 1.9:1 in Platt et al. 2009, 1:1 in Cedeño-Vázquez and Pérez-Rivera 2010, 1.6:1 in Suárez-Coya et al. 2013). Sex ratio when only considering wild crocodiles in our dataset was 1.6:1 (male:female), which also did differ from the

studies mentioned above. Threshold estimates generated by RTM were consistent across all three crocodile length measures tested (TL, SVL, CL) and were able to highlight four length intervals with well-defined thresholds, likely to correspond to significant development stages in *C. moreletii*. These length intervals seem to correspond to important ontogenetic changes in this species. Length class I and II (crocodiles < 891 mm TL) include young individuals which exhibit mainly a lengthwise growth pattern (i.e. length is prioritized over girth). When crocodiles enter length class III (TL ≥ 891 mm), their body mass starts to increase significantly and surpasses longitudinal growth rate (size). Evidence of ontogenetic changes have also been reported in the common snapping turtle *Chelydra serpentina*, where individuals exhibit a decrease in longitudinal growth rate upon reaching sexual maturity (Christiansen and Burken 1979, Galbraith et al. 1989). For *C. moreletii*, a recent study reports that the onset of genital maturity in males starts at approximately 1300 mm TL (Moore et al. 2019), which corresponds to length class III in our RTM. Morphological analysis of our dataset suggests that development of secondary sexual characteristics in *C. moreletii* initiates in length class III, where sexual maturity is also achieved. On the other hand, field observations indicate that only a small proportion of females is reproductively active before transitioning into adulthood (size class IV; Platt et al. 2008, Casas-Andreu et al. 2011).

Nesting behavior has been reported in *C. moreletii* females exhibiting TL ranging from 1210 mm to 1350 mm in the wild (Platt et al. 2008, Casas-Andreu et al. 2011), but reproductive size has been generally established at 1500 mm TL (Platt et al. 2008, 2009, Barrios-Quiroz et al. 2012). These smaller sizes of 1210 mm and 1350 mm for a reproductive female were estimated based on analysis of egg measurements, and suggest that females may be reproductively active at a size lengths < 1498 mm. Reproductive behavior is also thought to be influenced by other environmental and social components, such as the presence of dominant females preventing smaller animals to copulate; or vice versa, in the absence of larger dominant females, smaller females

Table 2. Geometric mean of body mass (W) and threshold values of total length (TL), snout-vent length and cranial length (CL) within each length class interval of *C. moreletii* identified through regression tree analysis.

Stage	TL (mm)	W (g)	SVL (mm)	W (g)	CL (mm)	W (g)
I	< 514	117	< 239	107	< 81.05	119
II	< 891	802	< 434	698	< 134.5	847
III	< 1497.5	4356	< 746	4148	< 213	4709
IV	≥ 1497.5	28	≥ 746	29 491	≥ 213	27 190
		953				

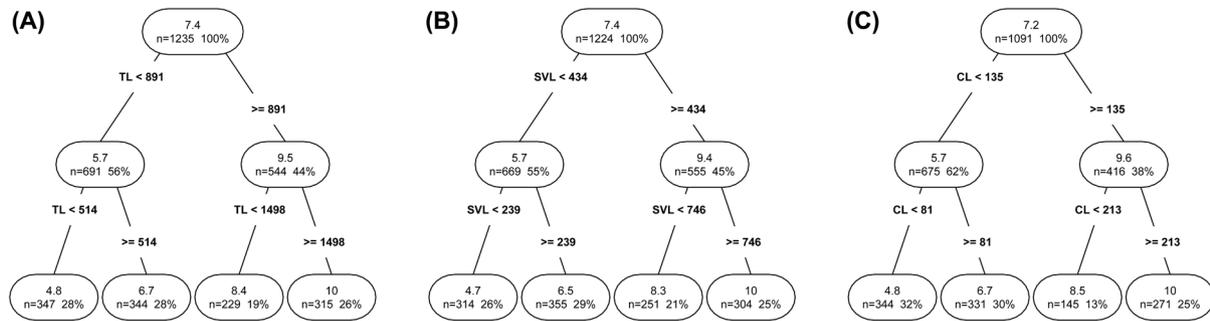


Figure 4. Regression tree models of crocodile body weight. Predictor variable combinations tested were: (A) total length (TL), sex and origin (wild or captivity); (B) snout–vent length (SVL), sex and origin; (C) cranial length (CL), sex and origin.

may have an opportunity to reproduce (Tucker et al. 2006). For captive-reared crocodiles, it has been suggested that males are likely to reach sexual maturity at similar lengths as females (Platt et al. 2009). As such, the length class IV ( $\geq 1498$  mm TL) determined by the RTM can then represent the overall threshold size where individuals complete their sexual maturation and, physiologically, are able to be reproductively active. However, current knowledge on sexual maturation in *C. moreletii* is still incipient and future studies addressing it are still required to fully understand the ecological and physiological factors influencing it.

A strong allometric relationship was observed between TL and SVL ( $R^2=0.98$ ) through our analysis, which did seem to be affected by crocodile gender. Our data analysis also demonstrated that one is able to use either TL or SVL as an indicator of length in *C. moreletii*. However, caution should be taken when TL is used as a measure of length as some individuals could exhibit tail mutilations (which is not that uncommon in larger individuals), in order to avoid size underestimation. In such cases, we recommend the use of SVL as the primary length measure then estimate TL based on the relationship equations provided by this study.

One of the major assumptions in our study was that sex and size class were equally represented within the dataset to avoid any possible masked results induced by unequal representation of morphological data between gender and length class intervals due to sampling bias. For example, detection probability of hatchlings (class I) are generally much higher in months following the end of nesting season than during the rest of the year, due to their high mortality rates. Juvenile individuals (class II) have a significantly lower mortality rates, which keeps decreasing as crocodiles grow in length (Thorbjarnarson 1997). Differences in detection probabilities have also been reported for size classes III and IV (sub-adults and adults) due to behavioral and habitat preference between males and females (Rosenblatt and Heithaus 2011). As our morphological dataset contains an elevated sample

size ( $n=1266$ ) with balanced sex and size ratios with no apparent significant difference amongst groups we are confident that the equality assumption was met.

The absence of significant differences in the length versus body mass relationships between males and females and between wild and captive crocodiles suggest that sexual maturity is more closely associated with body size than age, which has already been reported for *C. moreletii* in Belize (Platt et al. 2009), *Alligator mississippiensis* (Wilkinson and Rhodes 1997) and also in other vertebrate groups (Blueweiss et al. 1978). Despite the relationship between TL and body mass not differing between sexes (i.e. male and female crocodiles of similar length will also exhibit similar body mass), maximum body mass registered for a *C. moreletii* male is approximately 15% higher than for a female. This disparity in body mass is likely associated with the fact that mature females invest more energy in reproduction than growth (Tucker et al. 2006, Platt et al. 2009). Furthermore, smaller adult males are less likely to reproduce (due to competition with larger males) and so there is larger energy investment growth, in order to improve their chances of reproduction (Barrios-Quiroz et al. 2012).

Our results demonstrate that *C. moreletii* exhibits sexual dimorphism, defined by the significant difference observed in the TL–CL and SVL–CL relationships between males and females. Similar results have been reported for *A. mississippiensis* (Woodward et al. 1995). Male *C. moreletii* individuals tend to exhibit shorter head lengths (relative to body size) when compared to females of the same size. This relationship is different amongst identified length classes (although it is not clear from our analysis if the observed differences are also present between sexes within each length class), which indicates that the relation between head size and body size decreases as crocodiles grow in size, particularly in length class IV. Sexual dimorphism in *C. moreletii* has been reported in Belize (Platt et al. 2009), based on an index of dimorphism in body size (Lovich and Gibbons 1992) and maxillary

Table 3. Comparison between *Crocodylus moreletii* size class categories based on total length (in millimeters) used in previous studies and the length class intervals based on threshold values estimated through identified by our regression trees. All values are expressed in millimeters.

Class (stage)	Life stage	Platt et al. 2006.	Padilla et al. 2009	Cedeño-Vázquez et al. 2011	This study
Hatchlings	hatchlings	< 300		< 300	
I	yearlings	$\geq 300$ ; $\leq 500$	< 500	$\geq 300$ ; $\leq 500$	< 514
II	juveniles	$> 500$ ; $\leq 1000$	$> 501$ ; $< 1000$	$> 500$ ; $\leq 1000$	$\geq 514$ ; $< 891$
III	sub-adults	$> 1000$ ; $\leq 1500$	$> 1001$ ; $< 1500$	$> 1000$ ; $\leq 1500$	$\geq 891$ ; $< 1497$
IV	Adults	$> 1500$	$> 1501$	$> 1500$	$\geq 1497$

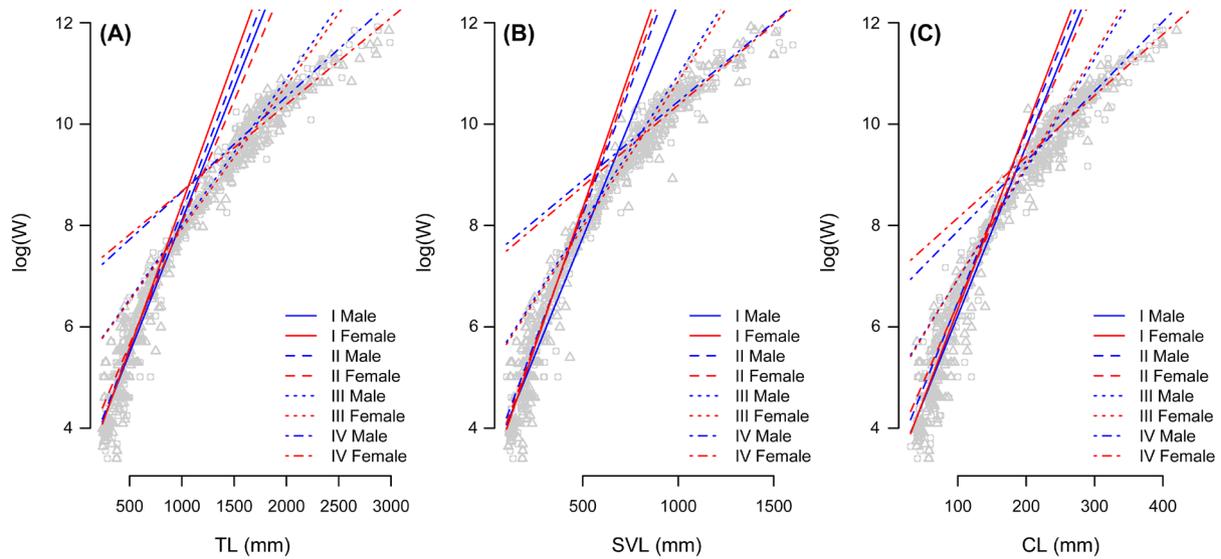


Figure 5. Dispersion between the logarithm of crocodile body mass (LogW) and: (A) total length (TL); (B) snout–vent length (SVL); (C) cranial length (CL). Solid and dashed lines represent, respectively, the linear models estimated for different length class intervals identified in the regression tree analysis. Blue and red colors represent males and females respectively. All lengths are expressed in millimeters.

and mandibular teeth (Moore et al. 2019). Furthermore, it is known that overall *C. moreletii* males are significantly larger than females (a feature shared amongst crocodylian species; Grigg and Kirshner 2015) and that the slope of the TL–CL relationship decreases with crocodile size in males, whereas in females it increases (Barrios-Quiroz et al. 2012). Head morphology is known to be related to foraging strategy and prey dimensions (Blanco et al. 2015), and so variations in its relationship with body size might be a response to ontogenetic changes in diet (Monteiro et al. 1997, Erickson et al. 2003). In *C. moreletii*, it has been reported that smaller crocodiles feed mostly on insects and crustaceans. As the crocodiles of this species grow in size there is an increase in the consumption of vertebrates (Platt et al. 2006).

We did not find a significant difference between wild and captive-reared crocodiles, which indicates that captivity does not induce significant expression of morphological characters in addition to an overall faster growth rate due to higher food availability (Serna-Lagunes et al. 2010, Barrios-Quiroz et al. 2012). Maxillary and mandibular teeth have been reported to exhibit a more robust growth in males when they reach a

size of 650 mm SVL (~1300 mm TL; Moore et al. 2019), which is in agreement with the TL–CL relationship observed in our data, further suggesting that sexual dimorphism differences in *C. moreletii* initiate in length class III but become more evident in length class IV.

Assignment of crocodylian individuals into groups or classes based on size is a common practice in management strategies for both captive and free ranging animals. However, it is not uncommon for crocodylians of the same age to exhibit different sizes or vice versa (Wilkinson et al. 2016). Therefore, aging crocodylians in the wild is extremely difficult and impractical. As such the use of ‘age’ has long been questioned as a reliable indicator of relevant aspects of individual development in a wild population (Caswell 2001). On the other hand, use of size classes in crocodylians is deemed much more relevant and practical to, for example, estimate the vital parameters in a population based on their life cycle, defined by a series of identifiable morphological stages (e.g. size; Manly 1990).

We would like to highlight the importance of morphometric data analysis to confirm the usage of size groups or

Table 4. Generalized linear model summary table of pairwise comparison values (t and p) in relation to difference in *C. moreletii* body mass (W) between length classes, sex and sex/length class, when using different length measurements (total length – TL; snout–vent length – SVL; cranial length – CL) as predictor variables.

Factor	Comparison	Total length		Ventral length		Cranial length	
Length class	I versus II	t=0.92	p=0.21	t=-0.20	p=0.83	t=0.70	p=0.14
	I versus III	t=7.68	p < 0.01	t=5.75	p < 0.01	t=4.59	p < 0.01*
	I versus VI	t=11.7	p < 0.01	t=9.94	p < 0.01	t=9.28	p < 0.01*
	II versus III	t=7.03	p < 0.01	t=7.67	p < 0.01	t=3.53	p < 0.01*
	II versus IV	t=11.4	p < 0.01	t=13.6	p < 0.01	t=7.63	p < 0.01*
	III versus IV	t=6.19	p < 0.01	t=8.04	p < 0.01	t=5.21	p < 0.01*
Sex	F versus M	t=0.35	p=0.73	t=-1.12	p=0.26	t=0.23	p=0.81
Sex/Length class	F I versus M I	t=-0.80	p=0.42	t=-1.23	p=0.21	t=-0.47	p=0.63
	F II versus M II	t=1.02	p=0.30	t=-0.37	p=0.70	t=0.54	p=0.58
	F III versus M III	t=0.20	p=0.84	t=0.15	p=0.87	t=-0.15	p=0.87
	F IV versus M IV	t=1.05	p=0.29	t=-0.25	p=0.8	t=1.24	p=0.21

\* Significant differences.

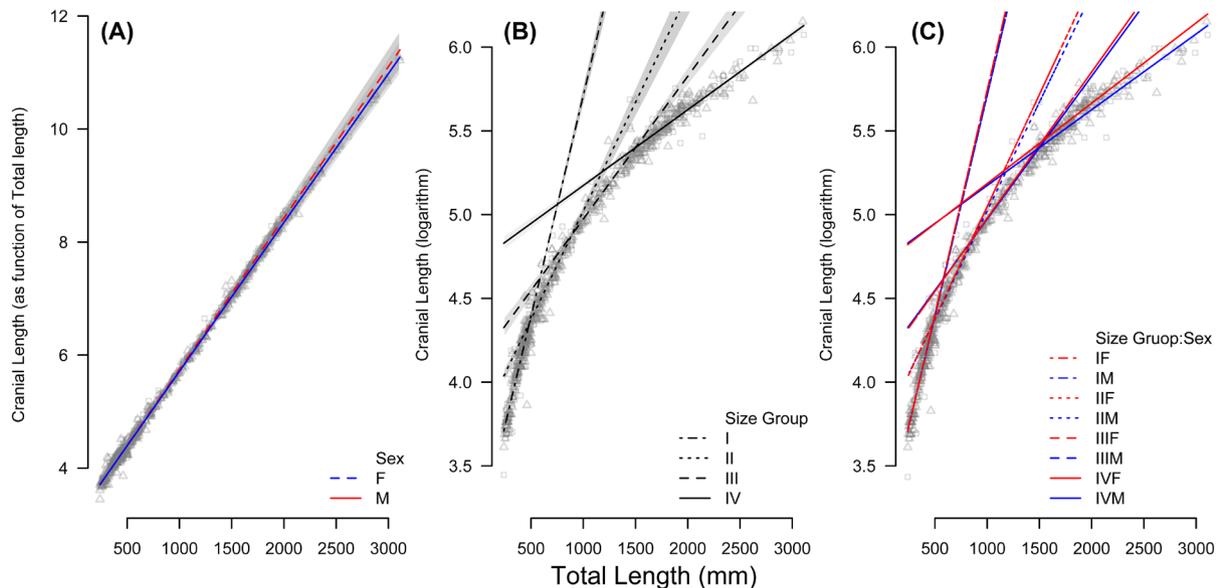


Figure 6. Total length (TL) and cranial length (CL) relationships in *C. moreletii* between (A) males and females; (B) length intervals; (C) sex:length class intervals.

classes in crocodylian species worldwide. In our study, we demonstrate that size intervals used for *C. moreletii* in previous population studies reflect the species growth patterns, but that might not be the case in all crocodylian species. We recommend researchers to use a similar approach to ours to test their data and verify if it matches size stage intervals defined and in use for ecological and management studies in those species.

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## References

- Barrios-Quiroz, G. et al. 2012. Sexual size dimorphism and allometric growth of morelet's crocodiles in captivity. – *Zool. Sci.* 29: 198–203.
- Blanco, R. E. et al. 2015. The 'death roll' of giant fossil crocodyliforms (Crocodylomorpha: Neosuchia): allometric and skull strength analysis. – *Hist. Biol.* 27: 514–524.
- Blueweiss, L. et al. 1978. Relationships between body size and some life history parameters. – *Oecologia* 37: 257–272.
- Casas-Andreu, G. 1986. Observaciones sobre los nidos y las nidadas de *Crocodylus moreletii* en México. – *Anal. Inst. Ciencias Mar.Limnol.* 13: 123–303, in Spanish.
- Casas-Andreu, G. et al. 2011. Reproducción en cautiverio de *Crocodylus moreletii* en Tabasco, México. – *Rev. Mex. Biodivers.* 82: 261–273, in Spanish.
- Caswell, H. 2001. Matrix population models: construction, analysis and interpretation, 2nd edn. – Sinauer, Sunderland, MA, USA.
- Cedeño-Vázquez, J. R. and Pérez-Rivera, S. D. 2010. El cocodrilo de pantano (*Crocodylus moreletii*) en Laguna Esmeralda, Quintana Roo, México. – *Rev. Latinoam. Conservación* 1: 91–98, in Spanish.
- Cedeño-Vázquez, J. R. et al. 2006. Population status and distribution of *Crocodylus acutus* and *C. moreletii* in southeastern Quintana Roo, México. – *Herpetol. Nat. Hist.* 10: 53–66.
- Cedeño-Vázquez, J. R. et al. 2011. Condición corporal del cocodrilo de pantano (*Crocodylus moreletii*) en el Río Hondo, Quintana Roo, México. – *Quehacer Científico en Chiapas* 1: 19–26, in Spanish.
- Cedeño-Vázquez, J. R. et al. 2014. *Crocodylus moreletii* (Morelet's Crocodile) diet. – *Herpetol. Rev.* 45: 322.
- Charrau, P. 2011. Estimación de la edad de los cocodrilos (*Crocodylus acutus*) de Banco Chinchorro, Quintana Roo, México. – *Quehacer Científico en Chiapas* 1: 36–43, in Spanish.
- Christiansen, J. L. and Burken, R. R. R. 1979. Growth and maturity of snapping turtle (*Chelydra serpentina*) in Iowa. – *Herpetologica* 35: 261–266.
- CONABIO 2015. Database of the Morelet's crocodiles (*Crocodylus moreletii*) monitoring programme; seasons 2011, 2012 and 2013; projects: SNIB-CONABIO JE007, JE008, JE009, JE010, LE01. Accessed 2 Dec 2015. – CONABIO, Mexico.

- Debeljak, M. and Džeroski, S. 2011. Decision trees in ecological modelling, pp. 197–209. – In: Jopp, F. et al. (eds), *Modelling complex ecological dynamics*. Springer.
- Emerson, S. B. 2000. Vertebrate secondary sexual characteristics – physiological mechanisms and evolutionary patterns. – *Am. Nat.* 156: 84–91.
- Erickson, G. M. et al. 2003. The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*). – *J. Zool.* 260: 317–327.
- Escobedo-Galván, A. H. et al. 2009. *Crocodylus moreletii* (Morelet's crocodile) nesting ecology. – *Herpetol. Rev.* 40: 211–212.
- Galbraith, D. A. et al. 1989. The influence of growth rate on age and body size at maturity in female snapping turtles (*Chelydra serpentina*). – *Copeia* 1989: 896–904.
- González-Jáuregui, M. et al. 2012. Persistent organic contaminants and steroid hormones levels in Morelet's crocodiles from the southern Gulf of Mexico. – *Arch. Environ. Contamin. Toxicol.* 62: 445–454.
- Grigg, G. and Kirshner, D. 2015. *Biology and evolution of crocodylians*. – CSIRO Publishing, Melbourne, Australia.
- Hunt, R. H. 1975. Maternal behavior in the morelet's crocodiles, *Crocodylus moreletii*. – *Copeia* 1975: 763–764.
- Hunt, R. H. 1977. Aggressive behavior by adult morelet's crocodiles *Crocodylus moreletii* toward young. – *Herpetologica* 33: 195–201.
- Logan, M. 2010. *Biostatistical design and analysis using R*. – Wiley-Blackwell.
- Lovich, J. E. and Gibbons, J. W. 1992. A review of techniques for quantifying sexual size dimorphism. – *Growth Devel. Aging* 56: 269–281.
- Manly, B. F. J. 1990. Stage-structured populations, sampling, analysis and simulation. *Population and community biology series*. – Chapman and Hall.
- McHenry, C. R. et al. 2006. Biomechanics of the rostrum in crocodylians: a comparative analysis using finite-element modeling. – *Anatom. Rec. A Discov. Mol. Cell. Evol. Biol.* 288: 827–849.
- Messel, H. et al. 1981. Surveys of tidal rivers systems in the northern territory of Australia and their crocodile population. – Pergamon Press.
- Monteiro, L. R. et al. 1997. Comparative ontogenetic shape changes in the skull of Caiman species (*Crocodylia, Alligatoridae*). – *J. Morphol.* 231: 53–62.
- Moore, B. C. et al. 2019. Correlation between increased postpubertal phallic growth and the initiation of cranial sexual dimorphisms in male Morelet's crocodile. – *J. Exp. Zool. A Ecol. Integr. Physiol.* 331: 562–570.
- Padilla, S. E. et al. 2009. Comparison of sodium and lithium heparin anticoagulants in plasma biochemistry of Morelet's crocodiles (*Crocodylus moreletii*) in Campeche, México. – *Vet. México* 40: 203–211.
- Padilla, S. E. et al. 2010. Estudio de caso: el cocodrilo de pantano *Crocodylus moreletii* en la Reserva de la Biosfera Los Petenes, Campeche. – In: Villalobos-Zapata G. J. and Mendoza-Vega, J. (eds), *La Biodiversidad en Campeche: Estudio de Estado*. CONABIO, México, pp. 344–348, in Spanish.
- Platt, S. G. et al. 2006. Food habits, ontogenetic dietary partitioning and observations of foraging behavior of Morelet's crocodile (*Crocodylus moreletii*) in northern Belize. – *Herpetol. J.* 16: 281–290.
- Platt, S. G. et al. 2008. Reproductive dynamics of a tropical freshwater crocodylian: Morelet's crocodile in northern Belize. – *J. Zool.* 275: 177–189.
- Platt S. G. et al. 2009. Size estimation, morphometrics, sex ratio, sexual size dimorphism and biomass of Morelet's crocodile in northern Belize. – *Caribbean J. Sci.* 45: 80–93.
- Rosenblatt, A. E. and Heithaus, M. R. 2011. Does variation in movement tactics and trophic interactions among American alligators create habitat linkages? – *J. Anim. Ecol.* 80: 786–798.
- Rutherford, A. 2011. *ANOVA and ANCOVA: a GLM approach*, 2nd edn. – Wiley.
- Sánchez-Herrera, Ó. et al. 2011. Programa de Monitoreo del Cocodrilo de Pantano (*Crocodylus moreletii*). – CONABIO – SEMARNAT, Mexico, in Spanish.
- Serna-Lagunes, R. et al. 2010. Morphological variability and body growth on four populations of *Crocodylus moreletii* in captivity. – *Rev. Mex. Biodivers.* 81: 713–719.
- Suárez-Coya, M. et al. 2013. Variation in size class and sex ratio of Morelet's crocodile in wetlands of Campeche, México. – *Herpetol. Conserv. Biol.* 8: 447–455.
- Therneau, T. et al. 2019. rpart: recursive partitioning and regression trees. – R package ver. 4.1-15. <<https://CRAN.R-project.org/package=rpart>>, accessed 27 July 2020.
- Thorbjarnarson, J. B. 1997. Are crocodylian sex ratios female biased? The data are equivocal. – *Copeia* 1997: 451–455.
- Tucker, A. D. et al. 2006. Growth dynamics of freshwater crocodiles (*Crocodylus johnstoni*) in the Lynd River, Queensland. – *Aust. J. Zool.* 54: 409–415.
- Verdade, L. M. 2000. Regression equations between body and head measurements in the broad-snouted caiman (*Caiman latirostris*). – *Rev. Bras. Biol.* 60: 469–482.
- Wallace, K. M. and Leslie, A. J. 2008. Diet of the Nile crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. – *J. Herpetol.* 42: 361–368.
- Warnes, G. R. et al. 2018. gmodels: various R programming tools for model fitting. – R package ver. 2.18.1. <<https://cran.r-project.org/web/packages/gmodels/index.html>>, accessed 27 Sep 2017.
- Wilkinson, P. M. and Rhodes, W. E. 1997. Growth rates of American alligators in coastal South Carolina. – *J. Wildl. Manage.* 61: 397–402.
- Wilkinson, P. M. et al. 2016. Determinate growth and reproductive lifespan in the American alligator (*Alligator mississippiensis*): evidence from long-term recaptures. – *Copeia* 104: 843–852.
- Woodward, A. R. et al. 1995. Maximum size of the alligator (*Alligator mississippiensis*). – *J. Herpetol.* 29: 507–513.
- Ziegler, T. and Olbort, S. 2007. Genital structures and sex identification in crocodiles. – *Crocodylian Specialist Group Newsl.* 26: 16–17.