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INDIRECT MORPHOLOGICAL MEASURES TO INFER BODY SIZE IN A WILD POPULATION OF THE CHIAPAS SPECTACLED CAIMAN, *CAIMAN CROCODILUS CHIAPASIUS* (BOCOURT, 1876)

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***Abstract*.—Several indirect measures (photographs, tracks, skulls) and remote techniques (nocturnal spotlight surveys) have been suggested as ways to estimate body size in crocodilians; however, the analysis of this kind of data does not fit the basic assumptions of the statistical allometric approach. We tested the utility of these techniques to infer body size from head and left foot measurements from a wild population of a subspecies of the Spectacled Caiman (*Caiman crocodilus chiapasius*) in Chiapas, Mexico using an allometric approach. We also tested for sexual size dimorphism using total length and snout-vent length. We only found sexual size dimorphism in total length. We also found that the snout length, inter-orbital width, and foot length have an isometric correlation with body size (total length or snout-vent length). Snout length and foot length measurements explained 65 to 74% of the body size variance when we analyzed overall data or only data from males, and seem to be useful to infer body size in this species. We suggest a conservative and species-specific use of indirect or remote measurements to estimate body size in crocodiles.**

Key Words.—allometric correlations; body size; *Caiman crocodilus chiapasius*; isometry; Spectacled Caiman

INTRODUCTION

Monitoring crocodile populations represent a challenge in the design of proper methods that allow the collection of good data. Capturing crocodiles is a difficult task, and amassing large samples sizes takes much time and money. For this reason, techniques have been designed to obtain data from indirect sources such as collections of skulls, estimating body size from heads seen during nocturnal spotlight surveys, the use of skins found in markets, and the use of photographs and tracks (Webb and Messel 1978; Montague 1984; Platt et al. 2009; Webb et al. 2012). These techniques have been considered the preferred methodology in monitoring plans (Montague 1984; Piras et al. 2009; Sanchez-Herrera et al. 2011) and even have been used to infer correlations with life-history traits (Wilkinson and Rice 2000; Platt et al. 2008).

Body size, age, and sex are the primary data needed to develop growth and demographic models (Caswell 2001), which are the basic information needed to achieve successful wildlife conservation and management programs (Primack 2002). Several indirect measurements and methods have been developed to assess the body size (and sometimes sex) in crocodiles without capturing the animals. Two techniques that are commonly used are snout-eye distance (distance between the tip of snout and the end of cranial bones) and the distance between eyes (inter-orbital width), commonly estimated in nocturnal spotlight surveys (Bourquin 2008). Similarly, length and width of footprints (tracks) have been used as estimators of body size (Montague 1984; Verdade 2000, 2003; Platt et al. 2009).

Inferring body size, sex, and even age from indirect measurements have important (and deep) assumptions that must be met for the data to be reliable for use in demographic and population growth models: (1) there is actual sexual size dimorphism in the species studied (even in immature individuals); (2) the indirect estimators such as footprints or head measurements have an isometric correlation with body size and should explain a considerable amount of the body size variance for the indirect technique to be statistically accurate; and finally, (3) body size must be a proper estimator of age. All these assumptions are difficult or even impossible to attain because there is no way to distinguish sex from body size in immature (small) individuals (Barrios-Quiroz et al. 2012), body size of adult males and females overlaps in a broad range of size classes, and there is considerable evidence supporting high variation in body size for a given age in crocodilians (Platt et al. 2009; Casas-Andreu et al. 2011; Barrios-Quiroz and Casas-Andreu 2011; Barrios-Quiroz et al. 2012). Although these assumptions can be hard to meet, they can be used as a framework to adjust indirect methodologies to improve the accuracy of the data collected.

TABLE 1. Indirect morphological measures to infer body size (TL or SVL, specified below species name) in crocodilians. Abbreviations are DCL = dorsal cranial length, IOW = inter-orbital width, SL = snout length, RTL = rear-foot track length, RTW = rear-foot track width; I = 150–200 cm, II = 200.1–250 cm, H = hatchlings, A = adults, S = sub-adults, a = intercept, b = slope, n = sample size, n/a = not available. Those values are considered in the broad or qualitative sense because the size definition for these classes is different between papers. Readers should consult original citation for details.

Species	Age	Wild/Captivity	Measure	a	b	r^2	n	Source
Crocodylus moreletii	I	Captivity	RTL	102.20	5.20	0.50	121	Barrios-Quiroz et al. 2012
(TL)	I	Captivity	RTW	100.60	7.80	0.50	121	Barrios-Quiroz et al. 2012
	II	Captivity	RTW	130.60	9.30	0.60	121	Barrios-Quiroz et al. 2012
	I	Captivity	DCL	37.40	5.50	0.90	121	Barrios-Quiroz et al. 2012
	II	Captivity	DCL	67.50	4.90	0.70	121	Barrios-Quiroz et al. 2012
Crocodylus porosus	H, S, A	Wild	foot width	-0.10	13.87	n/a	184	Webb and Messel 1978
(SVL)	H, A	Wild	hand width	-8.20	12.12	n/a	184	Webb and Messel 1978
	H, A	Wild	SL	3.27	4.82	n/a	619	Webb and Messel 1978
	H, A	Wild	head length	-1.38	3.32	n/a	617	Webb and Messel 1978
	H, A	Wild	IOW	16.30	34.92	n/a	225	Webb and Messel 1978
Caiman latirostris	A	Wild	SL	21.60	-0.32	0.96	29	Verdade 2000
(SVL)	A	Wild	IOW	4.50	4.48	0.87	29	Verdade 2000
	A	Wild	DCL	-3.78	0.48	0.96	29	Verdade 2000
	A	Captivity	SL	1.42	0.91	0.99	120	Verdade 2000
	A	Captivity	IOW	7.52	4.14	0.95	120	Verdade 2000
	A	Captivity	DCL	-6.35	0.52	0.99	120	Verdade 2000
Alligator sinensis	S, A	Captivity	SL	-0.86	0.84	0.95	98	Wu et al. 2006
(SVL)	S, A	Captivity	IOW	-0.06	6.84	0.79	98	Wu et al. 2006
	S, A	Captivity	DCL	-5.32	0.47	0.95	98	Wu et al. 2006
Crocodylus novaeguineae	H, A	Wild	hand width	13.32	11.46	0.66	923	Montague 1984
(SVL)	H, A	Wild	foot width	11.00	7.78	0.67	923	Montague 1984
	H, A	Wild	IOW	8.98	46.70	0.80	1,037	Montague 1984
	H, A	Wild	SL	4.81	4.78	0.92	1,037	Montague 1984

Several studies of crocodilians have used indirect measurements of body size with apparent success to infer body size (Table 1). Some even have used these indirect techniques to test correlations of body size with reproductive traits with good results (Platt et al. 2008; Platt et al. 2009, but see Casas-Andreu et al. 2011), although others found less accurate results (Barrios-Quiroz et al. 2012). The Spectacled Caiman (*Caiman crocodilus*) in southeastern Mexico is a species for which gathering population information by actual capture is prohibitive, and an indirect method of accurately determining population characteristics would be useful. The Spectacled Caiman is a mid-sized alligatorid, with males reaching 2.5 m total length (TL) and females 1.4 m (Cifuentes and Cupul 2004). Álvarez del Toro (1974) reported that males have larger and wider heads than females. Spectacled Caiman range from northern Mesoamerica on the coast of Oaxaca to the center of South America (Vasconcelos et al. 2006). It is found in both the Atlantic and Pacific basins and very deep into South America through the Rio Paraguay, Amazon Basin, and the northern part of Argentina (Vasconcelos et al. 2006). Spectacled Caiman live from large aquatic habitats such as lakes, lagoons, and rivers to small ponds and swamps.

The subspecies *C. caiman chiapasius* ranges from the coast of central Oaxaca to the Pacific coast of Nicaragua (Escobedo-Galvan et al. 2011) and represent the northern distribution of the species. We captured individuals of this subspecies and recorded a variety of body and skull measurements. We tested if body size and sex of *Caiman crocodilus chiapasius* could be estimated reliably using remote methods (visual estimation of snout-eye distance or distance between eyes) and indirect techniques (tracks or foot impressions in river banks).

MATERIALS AND METHODS

We captured *Caiman crocodilus chiapasius* from February 2004 to May 2005 in the wetlands of the Pacific Coast of Chiapas, in the “Encrucijada” Biosphere Reserve, at the Municipality of Pijijiapan Chiapas (15°32´24”N, 93°11´16”–93°13´34”W), Mexico (Fig. 1). This region is a huge wetland system (144,848 ha) comprised of rivers, streams, swamps, lagoons, and seasonal ponds. The Chiapas Soconusco region annually receives 4,000 mm of precipitation (García 1973). The rainy season begins in May and extends through November (Instituto Nacional de Ecologia1999; Instituto

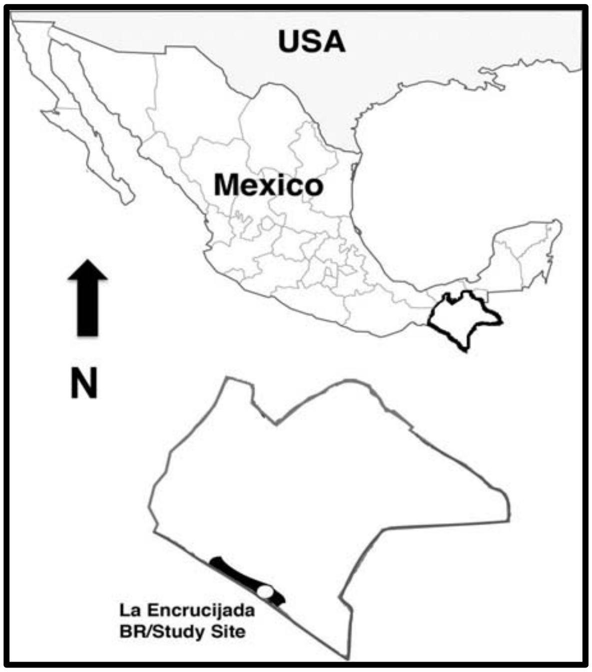

FIGURE 1. Map of the study site in Chiapas, Mexico where we studied a population of *Caiman crocodilus chiapasius*. The shaded area represents the polygon of the Encrucijada Biosphere Reserve. The study site is marked by a white dot.

Nacional de Estadistica y Geografia 2000). These water systems flood during the rainy season. The prevalent and typical habitats of the study site consisted of a network of small rivers and streams. Typical of this system are many patches of aquatic vegetation that support diverse aquatic fauna such as several species of fish, the American Crocodile (*Crocodylus acutus*), several species of turtles (*Claudius angustatus*, *Staurotypus salvinii*, and *Trachemys venusta*), and aquatic birds and mammals (Álvarez del Toro 1974; Instituto Nacional de Ecología 1999).

We captured Caimans in a small seasonal pond and in a perennial lagoon located at 2.5 km from the pond, in the southeast of the Reserve. We traversed the wetland system three days each month, and spent three hours per day collecting crocodiles starting half an hour before sunset. We used a small boat (cayuco) to move among the aquatic systems. Caimans were captured by noosing and we pulled captured individuals into the boat to take body size measurements with a 300 cm flexible ruler (to the nearest 1 cm) and weighed them with spring scales (Pesola® AG, Baar, Switzerland) to the nearest 1 kg. We recorded snout-vent length (SVL), total length (TL), and body mass (BM). SVL is the linear distance from the anterior margin of the cloaca to the anterior tip of the snout. TL is the distance from the tip of the snout to the tip of the tail measured by laying a ruler over the animal. We also recorded inter-orbital width (IOW), snout length (SL), and length of the left foot (FL) as additional measurements. Inter-orbital width is the shortest distance measured between the medial borders of the external bony orbits; SL is the distance from the tip of the snout to a line joining the anterior margins of the external orbits; and FL is the length from the tip of the longest toe to the back of the 'heel' with the foot flexed to approximate the footprint that each foot would make (Fig. 2). We determined sex by cloacal exploration and all individuals were permanently marked by caudal scale notching. Finally, we released captured animals in the same spot where they were caught. No caiman were harmed or died during handling over the course of the study.

To test for sexual size dimorphism, we compared the body size estimates (BM, SVL, hand TL) between males and females with Student *t* tests. We compared head measurements and FL between males and females using ANCOVA with the TL as covariate. We used Platt et al. (2009) definition of sexual size dimorphism as "a statistically significant difference in mean length or mass of sexually mature organisms from the same population during a time interval." To attain a reliable sample size for allometric analyzes, we combined data of males and females. For the allometric analyses, we follow Kings' (2000) methodology for correlations between body size (SVL or TL or BM) with other morphologic measures (FL, SL, and IOW). Data were transformed to a log-log function to meet allometric assumptions of linearity.

For the hypothesis testing and decision making, we followed Charnov (1993) in the use of simple regressions to test for isometry (null hypothesis) or hypo/hyperallometry (King 2000); we also follow Ryan and Lindeman (2007) in expecting a slope of 3.0 for regressions with a volumetric measure such as SL on BM, and a slope of 1.0 when regressions involve the analysis of two linear measures (e.g., SVL on IOW). We considered a slope with a 95% confidence interval (CI) positioned below the expected value as a significantly hypoallometric relationship; slopes with a 95% CI including the expected value to be isometric, and slopes with 95% CI above the expected value to be significantly hyperallometric. We also reported the untransformed (non-log transformed) equation components following Webb et al. (2012) to provide an applicable inference to body size with indirect or remote observations. We calculated the standard error of the estimate as the mean square root of all residuals squared following Webb et al. (2012) and Zar (1999). On each variable we tested for normality using a Shapiro-Wilk test; this technique allows us to present a body size distribution among the sampled individuals. We follow Webb et al. (2012) using a 100-cm interval to generate the size distribution. We performed all statistical analyses in JMP version 5.0.1 (SAS Institute Inc. Cary, North Carolina, USA) at an $\alpha = 0.05$.

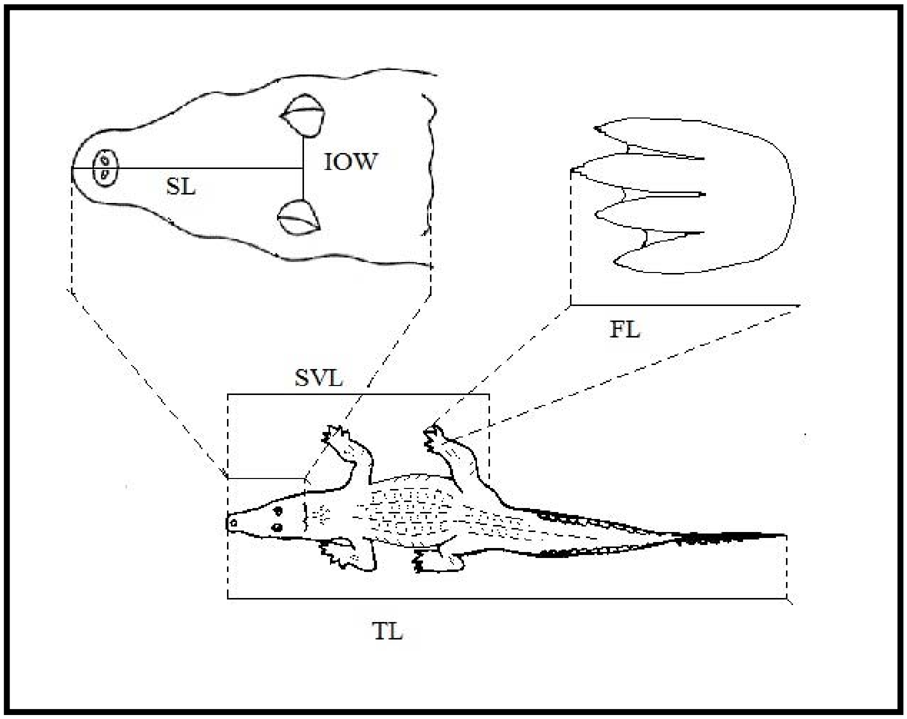

FIGURE 2. Morphological measurements recorded for the Spectacle Caiman (*Caiman crocodilus chiapasius*). Abbreviations are: SVL = snout-vent length, TL = total length, FL = left foot length, IOW = Inter-orbital width, and SL = snout length.

RESULTS

We caught 53 Spectacle Caiman (38 males and 15 females). Males ranged from 93–167 cm TL (mean = 135.32 cm) and females ranged from 77–143 cm TL (mean = 121.8 cm). Total length was normally distributed (Shapiro-Wilk test $W = 0.97$, $P = 0.36$) and body size distribution shows a preponderance of individuals between 110–150 mm TL (Fig. 3). For the six morphological traits measured, we only found variation between males and females in TL ($t = 2.38$, df = 51, $P = 0.02$), whereas the other estimators of body size did not show differences (Table 2). Snout-vent length and BM were nearly significant ($t = 1.18$, df = 51, $P = 0.06$ and $t = 1.73$, df = 51, $P = 0.08$, respectively), but head measurements and foot length did not show any variation between sexes (Table 2). Allometric analyses (Table 3) showed that in the overall data analysis, BM and IOW had hypoallometric correlations with TL and SVL. When we analyzed data for males only, we found only BM had a hypoallometric correlation with SVL and TL (Table 3). These allometric results showed that the percentage of body size variance explained (r^2) by indirect estimators such as IOW, SL, and foot length for TL range from 47 to 73%, and from 51 to 72% for SVL in the complete data set, and from 63 to 73% for TL and 75 to 64% for SVL in the male data set (Table 3). The most relevant indirect variables (non-transformed) that significantly explain TL were FL and SL for all data, and SL for males only data (Table 4). TL and SVL were directly related but SVL only explained 84% of TL variance (Table 4).

DISCUSSION

Sexual size dimorphism is ubiquitous in crocodiles (Fitch 1981). Males are typically larger than females in TL, BM, and SVL (Monteiro et al. 1997; Verdade 2000; Platt et al. 2009 Barrios-Quiroz et al. 2012). Our results pointed to sexual size dimorphisms when we use TL as an estimate of body size. Although not statistically significant at an alpha of 0.05, BM and SVL were nearly significant for sexual dimorphism. Sexual size dimorphism in crocodilians has been described as the result of ontological (Monteiro et al. 1997; Verdade 2003; Piña et al. 2007) and ecological processes (Platt et al. 2009), and the difference in body size between males and females has important life-history consequences directly related to sexual selection (Shine 1989; Cox et al. 2009; Cox and Calsbeek 2009).

The male skewed dimorphism in size of crocodiles apparently evolve from the typical polygynous mating system described for this reptile, when larger adult (and reproductive) males with massive and robust bodies are assumed to have greater chances of displacing other males to protect territory and breed (Platt et al. 2009).

TABLE 2. Morphometric comparison between male and female Spectacled Caiman (*Caiman crocodilus chiapasius*) in Chiapas, Mexico. Statistical comparisons used either the Student *t* test or ANCOVA (*F* values) and associated probability (*P*) values. Means are reported ± one standard deviation (SD).

Morphological variable	Test: *t*/*F*	*P*	Males (mean ± SD)	Females (mean ± SD)
Body mass	$t_{51} = 1.73$	0.08	12.21 ± 3.92 kg	10.20 ± 3.48 kg
Total length	$t_{51} = 2.38$	0.02	135.34 ± 18.30 cm	121.8 ± 19.43 cm
Snout-vent length	$t_{51} = 1.18$	0.06	72.40 ± 11.26 cm	66.16 ± 9.86 cm
Inter-orbital width	$F_{1,52} = 0.114$	0.90	4.96 ± 0.80 cm	4.53 ± 0.76 cm
Snout length	$F_{1,52} = 2.70$	0.10	12.02 ± 2.04 cm	10.26 ± 1.67 cm
Left foot length	$F_{1,52} = 0.022$	0.88	11.72 ± 2.04 cm	10.46 ± 1.84 cm

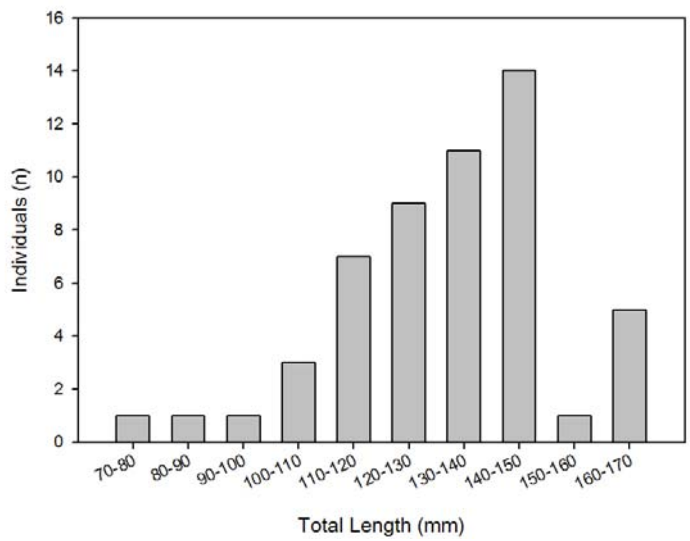

FIGURE 3. Body size (total length) distribution of the Spectacled Caiman (*Caiman crocodilus chiapasius*) in Chiapas, México based on a sample of 53 measured individuals.

One important finding in our male vs. female morphometric comparison was the lack of variation in the cranial measurements (IOW, SL) and FL. For this particular subspecies and population, this result implies that the cranial measurements we took were insufficient to describe sex, indicating that to discriminate between males and females there is a need to measure more cranial morphological variables such as described for *Caiman latirostris* (Verdade 2003; Piña et al. 2007).

The allometric analysis showed that the remote or indirect measurements used in this study showed isometric correlations with body size, which leads to a simpler and easier interpretation using linear equations (Charnov 1993). However, our data revealed that only FL and SL were useful measures to infer body size. From the morphological measurements we took, we consider FL as the most useful indirect measure to infer body size in surveys and monitoring programs (when conditions allow it) in *C. c. chiapasius*. Foot length explained 67–72% of body size variance and is easy and safe to measure with an ordinary ruler or other metric measurement device. However, tracks or foot impressions are highly dependent of substrate conditions (humidity and depth) and only should be used as a complementary source of data (Plat et al. 1990; Wilkinson and Rice 2000; Platt et al. 2009). Snout length also explained 69–74% of body size variation; nevertheless, the use of this indirect measurement should be conducted primarily on skulls and other remains, but not in nocturnal spotlight surveys as mere guessing based on researcher "experience of body size snout length correlation" as Sigler et al. (2011) noted. Snout

TABLE 3. Hypoallometric and isometric correlations between body size to head measurements and foot length (FL log transformed) in *Caiman crocodilus chiapasius* in Chiapas, Mexico. Abbreviations are TL = total length, SVL = snout-vent length, BM = body mass, IOW = inter-orbital width, SL = snout length.

X	Y	n	r^2	*P*	Expected slope under isometry	Slope	95% CL	Result	Y intercept
Overall									
TL	BM	53	0.79	< 0.001	3	2.28	1.95–2.60	Hypoallometry	-8.71
TL	IOW	53	0.47	< 0.001	1	0.75	0.53–0.97	Hypoallometry	-2.12
TL	SL	53	0.65	< 0.001	1	0.95	0.76–1.15	Isometry	-2.23
TL	Foot length	53	0.73	< 0.001	1	1.06	0.88–1.25	Isometry	-2.78
SVL	BM	53	0.86	< 0.001	3	2.31	2.04–2.57	Hypoallometry	-7.41
SVL	IOW	53	0.51	< 0.001	1	0.77	0.56–0.97	Hypoallometry	-1.70
SVL	SL	53	0.69	< 0.001	1	0.96	0.78–1.14	Isometry	-1.65
SVL	Foot length	53	0.72	< 0.001	1	1.04	0.86–1.21	Isometry	-2.00
Males only									
TL	BM	38	0.89	< 0.001	3	2.26	1.93–2.59	Hypoallometry	-8.63
TL	IOW	38	0.63	< 0.001	1	0.96	0.73–1.20	Isometry	-3.15
TL	SL	38	0.73	< 0.001	1	1.11	0.88–1.33	Isometry	-2.96
TL	Foot length	38	0.70	< 0.001	1	1.14	0.89–1.39	Isometry	-3.16
SVL	BM	38	0.84	< 0.001	3	2.03	1.74–2.35	Hypoallometry	-6.25
SVL	IOW	38	0.65	< 0.001	1	0.87	0.64–1.08	Isometry	-2.13
SVL	SL	38	0.74	< 0.001	1	1.00	0.80–1.20	Isometry	-1.82
SVL	Foot length	38	0.67	< 0.001	1	1.01	0.77–1.25	Isometry	-1.88

length as a remote indicator of body size should be used with calibrated photographs (Platt et al. 2009) or with high definition video, when SL could be inferred using the proper geometric morphology techniques.

When we compared our data with other studies (Table 1), our information differed in the amount of variance explained by the linear model. Most studies that infer body size from indirect, remote, or cranial measurements reported very high values of coefficients of determination. Our results do not showed very high r^2 values, and our data agree with those of Barrios-Quiroz et al. (2012), who reported middle to moderate values of r^2 for *Crocodylus moreletii*. Surprisingly our data differ from those of Webb et al. (2012), who found very high r^2 values (r^2 = 0.99) for a correlation between SVL to head length from fresh skins of *Caiman crocodilus* in Colombia.

We believe than an allometric approach (log-log regression and the contrast of the confidence interval for the observed slope with the expected slope; Charnov 1993; King 2000) should be used in all morphometric studies to make slopes comparable. Other study results did not reveal if the correlations were isometric or hyper/hypoallometric, which leads to a confused interpretation and even to the uncertainty of the straight line equation usage as a predictor of body size. We suggest that the isometric or allometric correlations between body sizes to indirect or remote measures (based in few variables) should be adjusted for the species under study. It appears that these correlations are species-specific, and allometric correlations should be translated again to their original data units to guarantee their direct applicability and usage for other researchers.

From the data we took on the field, FL and SL appear to be the most useful morphological measures to infer body size in the surveyed population of *C. c. chiapasius.* However, it seems that variation among these morphological traits is high within and between sub-species/populations (Webb et al. 2012); consequently, extrapolation should be conservative and derived from large sample size if possible and based on different age classes as suggested by Webb and Messel (1978) and Platt et al. (2009). We were unable gather a larger sample size to split our analysis into size classes, but based in the statistical properties of our data set, we

TABLE 4. Linear regression coefficients and equations between non transformed data of body size measurements (responses) correlated with indirect morphological measurements (predictors) in *Caiman crocodilus chiapasius* in Chiapas, Mexico. SEE is the standard error of the estimate. Abbreviations are TL = total length, SVL = snout-vent length, BM = body mass, IOW = inter-orbital width, SL = snout length.

Response (Y)	Predictor (X)	n	r^2	SEE	*P*	Slope (*b*x)	Intercept (*a*)
Overall							
TL	BM	53	0.80	1.69	< 0.001	0.1793	-11.94
TL	IOW	53	0.51	0.55	< 0.001	0.0300	0.89
TL	SL	53	0.68	1.67	< 0.001	0.0887	-0.15
TL	Foot length	53	0.71	1.09	< 0.001	0.0891	-0.36
TL	SVL	53	0.84	4.30	< 0.001	0.5267	1.37
SVL	BM	53	0.86	1.40	< 0.001	0.3239	-11.24
SVL	IOW	53	0.54	0.54	< 0.001	0.0537	1.04
SVL	SL	53	0.70	1.11	< 0.001	0.1575	0.40
SVL	Foot length	53	0.68	1.09	< 0.001	0.1522	0.61
Males only							
TL	BM	38	0.84	1.68	< 0.001	0.1969	-14.44
TL	IOW	38	0.65	0.55	< 0.001	0.0356	0.14
TL	SL	38	0.74	1.16	< 0.001	0.0960	-1.03
TL	Foot length	38	0.69	1.09	< 0.001	0.0932	-0.89
TL	SVL	38	0.83	4.27	< 0.001	0.5609	-3.51
SVL	BM	38	0.85	1.43	< 0.001	0.3224	-11.13
SVL	IOW	38	0.64	0.55	< 0.001	0.0574	0.80
SVL	SL	38	0.75	1.14	< 0.001	0.1578	0.60
SVL	Foot length	38	0.63	1.09	< 0.001	0.1454	1.19

consider our analysis accurate enough for the population surveyed. We recommend measuring more cranial features to infer body size and probable sex. But indirect estimates of body size should be measurable with a certain degree of accuracy, for example, in footprints and other tracks (e.g., tails, ventral part, etc.). Monitoring crocodiles should be conducted with standard protocols to make general comparisons. Protocols must be adapted to the special issues imposed by the species under study; however, to infer and predict important life-history traits such size or sex, the statistical procedures should be standardized to avoid guessing when comparing results.

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LITERATURE CITED

Álvarez del Toro, M. 1974. Los Crocodylia de México. Instituto Mexicano de Recursos, Renovables A.C., Chiapas, México.

Barrios-Quiroz, G., and G. Casas-Andreu. 2011. Crecimiento con diferentes dietas en crías de C*rocodylus moreletii* Dumeril Bibron & Dumeril 1851 (Crocodylia: Crocodylidae) en cautiverio, Tabasco, México. Latin American Journal of Conservation 1:104–111.

Barrios-Quiroz, G., G. Casas-Andreu, and. A.H. Escobedo-Galván. 2012. Sexual size dimorphism and allometric growth of Morelt's Crocodiles in captivity. Zoological Science 29:198–203.

Bourquin, S.L. 2008. The population ecology of the Nile Crocodile (*Crocodylus niloticus*) in the Panhandle Region of the Okavango Delta, Botswana. Ph.D. Dissertation, University of Stellenbosch, Stellenbosch, South Africa. 294 p.

Casas-Andreu, G., G. Barrios-Quiroz, and R. Macip-Ríos. 2011. Reproducción en cautiverio de *Crocodylus moreletii* en Tabasco, México. Journal of Mexican Biodiversity 82:261–273.

Caswell, H. 2001. Matrix Populations Models. Construction, Analysis, and Interpretation. Second Edition, Sinauer, Sunderland, Massachusetts, USA.

Cifuentes, J.L., and F.G. Cupul. 2004. ¿Los terribles cocodrilos? Fondo de Cultura Económica, México D.F., México.

Cox, R.M., and R. Calsbeek. 2009. Sex-specific selection and intraspecific variation in sexual size dimorphism. Evolution 64:798–809.

Cox, R.M., D.S. Stenquist, and R. Calsbeek. 2009. Testosterone, growth and the evolution of sexual size dimorphism. Journal of Evolutionary Biology 22:1586–1598.

Charnov, E.L. 1993. Life History Invariants. Some Explorations of Symmetry in Evolutionary Ecology. Oxford University Press, Oxford, UK.

Escobedo-Galvan, A., F.G. Cupul-Magaña, and J.A. Velasco. 2011. Misconceptions about distribution of

Caiman crocodilus chiapasius and *C. crocodilus fuscus* (Reptilia: Crocodylia: Alligatoridae). Zootaxa 3015:66–68.

Fitch, H.S. 1981. Sexual size differences in reptiles. Miscellaneous Publication No. 70. Museum of Natural History, University of Kansas, Lawrence, Kansas, USA.

García, E. 1973. Modificación al Sistema de Clasificación Climática de Köppen. Instituto de Geografía, Universidad Nacional Autónoma de México, México.

Instituto Nacional de Ecología. 1999. Programa de Manejo de la Reserva de la Biosfera la Encrucijada, SEMARNAT, México.

Instituto Nacional de Geografía y Estadística. 2000. Anuario Estadístico de Chiapas. INEGI-Gobierno del Estado de Chiapas. Tuxtla Gutiérrez, México.

King, R.B. 2000. Analyzing the relationship between clutch size and female body size in reptiles. Journal of Herpetology 34:148–150.

Montague, J.J. 1984. Morphometric analysis of *Crocodylus novaeguineae* from the Fly River drainage, Papua New Guinea. Australian Wildlife Research 11:395–414.

Monteiro, L.R., M.J. Cavalcanti, and H .J.S. Sommer III. 1997. Comparative ontogenetic shape changes in the skull of *Caiman* species (Crocodylia, Alligatoridae). Journal of Morphology 231:53–62.

Piña, C., A. Larriera, P. Siroski, and L.M. Verdade. 2007. Cranial sexual discrimination in hatching Broad-snouted Caiman (*Caiman latirostris*). Iheringia Série Zoológica Porto Alegre 97:17–20.

Piras, P., L. Teresi, A.D. Buscalioni, and J. Cubo. 2009. The shadow of forgotten ancestors differently constrains the fate of Alligatoroidea and Crocodyloidea. Global Ecology and Biogeography 18:30–40.

Platt, S.G., C.G. Brantley, R.S. Cropanzano, and R.W. Hastings. 1990. A method for determining the size of nesting female alligators. Wildlife Society Bulletin 18:296-298.Platt, S.G., R. Rainwater, J.B. Thorbjarnarson, A.G. Finger, T. Anderson, and S.T. McMurry. 2009. Size estimation, morphometrics, sex ratio, sexual size dimorphism, and biomass of Morelet's Crocodile in northern Belize. Caribbean Journal of Science 45:80-93.

Platt, S.G., T.R. Rainwater, J.B. Thorbjarnarson, and S.T. McMurry. 2008. Reproductive dynamics of a tropical freshwater crocodilian; Morelet's Crocodile in northern Belize. Journal of Zoology 275:177–189.

Primack, R.B. 2002. Essentials of Conservation Biology. Third edition. Sinauer, Sunderland, Massachusetts, USA.

Ryan, K.M., and P.V. Lindeman. 2007. Reproductive allometry in the Common Map Turtle *Graptemys geographica*. American Midland Naturalist 158:49–59.

Sanchez-Herrera, O., G. López Segurajáuregui, A. García-Naranjo Ortiz de la Huerta, and H. Benítez-Díaz. (Eds.). 2011. Programa de monitoreo del Cocodrilo de Pantano *(Crocodylus moreletii)*. México, Belice, Guatemala. CONABIO-SEMARNAT, México. 286 p.

Sigler, L., J.R. Cedeño-Vázquez, and F.G. Cupul-Magaña. 2011. Método de detección visual nocturna (DVN). Pp. 105–127 *In* Programa de Monitoreo del Cocodrilo de Pantano *(Crocodylus moreletii)*. México, Belice, Guatemala. Sanchez-Herrera, O., G. López Segurajáuregui, A. García-Naranjo Ortiz de la Huerta, and H. Benítez-Díaz. (Eds.). CONABIO-SEMARNAT, México.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. The Quarterly Review of Biology 64:419–461.

Vasconcelos, W.R., T. Hrbek, R. Da Silveira, B. de Thoisy, B. Marioni, and I.P. Farias. 2006. Population genetic analysis of *Caiman crocodylus* (Linnaeus, 1758) from South America. Genetics and Molecular Biology 29:220–230.

Verdade, L.M. 2000. Regressions equations between body and head measurements in the Broad-snouted Caiman (*Caiman latirostris*). Revista Brasileira de Biologia 60:469–482.

Verdade, L.M. 2003. Cranial sexual dimorphism in captive adult Broad-snouted Caiman (*Caiman latirostris*). Amphibia-Reptilia 24:92–99.

Webb, G.J., and H. Messel. 1978. Morphometric analysis of *Crocodylus porosus* from the north coast of Arnhem Land, Northern Australia. Australian Journal of Zoology 26:1–27.

Webb, G.J., M. Brien, C. Manolis, and S. Medrano-Bitar. 2012. Predicting total lengths of Spectacled Caiman (*Caiman crocodilus*) from skin measurements: a tool for managing the skin trade. Herpetological Conservation and Biology 7:16–26.

Wilkinson, P.M., and K.G. Rice. 2000. Determining the size of American Alligators using hind-foot track length. Proceedings Annual Conference Southeastern Association of Fish and Wildlife Agencies 54:337–340.

Wu, X.B., H. Hue, L.S. Wu, J.L. Zhu, and R.P. Wang. 2006. Regression analysis between body and head measurements of Chinese Alligators (*Alligator sinensis*) in the captive populations. Animal Biodiversity and Conservation 29:65–71.

Zar, J.H. 1999. Biostatistical Analysis. 4th Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

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The remaining authors did not provide biographical sketches.