

# Phenotypic Variability and Heritability of the Cephalic Region of *Caiman latirostris*

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**ABSTRACT** The study of the cephalic shape of crocodylian is relevant in the fields of ecology, systematics, evolution, and conservation. Therefore, the integration of geometric analysis within quantitative genetics allows the evaluation of the inheritable shape components. In this study, the dorsal cephalic region of 210 *Caiman latirostris* hatchlings was analyzed from seven populations in Santa Fe, Argentina, to detect intra- and inter-population phenotypic variability, and to determine the heritability of biological shape and size, using newly available geometric morphometric tools. The principal component analysis showed two configurations of cephalic shape that could be related to sexual dimorphism. In the canonical variate analysis, Procrustes distances between groups indicated that there are differences in shape among populations. Furthermore, the method of partial least squares indicated a covariation between cephalic shape and environmental variables. Regarding to CS of the skull we found significant differences among populations, moreover the partial least squares was also significant. Estimates of the heritability of shape and size were high, indicating that the components of these features are susceptible to the selection. *J. Morphol.* 277:370–378, 2016.

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**KEY WORDS:** broad-snouted caiman; morphology; quantitative genetics; phenotypic variability

## INTRODUCTION

*Caiman latirostris*, commonly known as “broad-snouted caiman” belongs to the Alligatoroidea (Brochu, 1999, 2003) and it is one of the two crocodylian species living in Argentina (Larriera, 1995). Wild populations of *C. latirostris* in Santa Fe province (Argentina) are subject of a sustainable use program called Proyecto Yacaré (Gob. de Santa Fe/MUPCN) and the species is listed in appendix II of CITES (Larriera et al., 2008).

The crocodylian skull has been intensely studied for many years (Brochu, 2001; Pierce et al., 2008; Bona and Desojo, 2011; Holliday et al., 2013; Clarac et al., 2015). The skull’s shape is relevant in the fields of ecology, behavior, evolution, and conservation of this species (Ouboter, 1996; Brochu, 2001; McHenry et al., 2006; Sadleir and Makovicky, 2008).

Morphometrics is the study of the shape variation and covariation with other variables. Geometric morphometric tools have succeeded not only to objectify the quantitatively assessment of morphological changes but also a qualitative assessment through recovery of the shape under study independent of size (Toro et al., 2010). Given the richness of the information extracted from geometric morphometric methods, a natural extension would involve the assessment of the heritable component of shape as defined by geometric descriptors. Such effort would require the integration of geometric procedures of shape description into the framework of quantitative genetics (Monteiro et al., 2002; Klingenberg and Monteiro, 2005).

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Fig. 1. *Caiman latirostris*, placement of 18 landmarks representing the dorsal cephalic region.

Furthermore, the environmental conditions experienced during early ontogeny affect embryos (Arnqvist and Johansson, 1998). Thus, environmental conditions during embryogenesis can induce phenotypic variation in animals. Temperature is a particularly important factor in determining developmental rates and final size in ectotherms (Braña and Ji, 2000).

Morphometric studies of caimans in the framework of quantitative genetics are not frequent (Verdade, 2000; Amavet et al., 2009). Most studies about morphology and crocodylian growth conducted so far are only related to the size of the animals [e.g., Allsteadt and Lang (1995); Braña and Ji (2000); Piña et al. (2007a); Parachú Marcó et al. (2010)] but they do not consider the shape. Geometric morphometric as used here extends the analysis of the morphology of individuals.

The aim of this work is to study Argentinean populations of *C. latirostris* to detect intra- and inter-population phenotypic variability and to determine the heritability of biological shape and size in the dorsal cephalic region. Information obtained could be used to adjust and provide

important data for sustainable use of *C. latirostris* programs and related species.

## MATERIALS AND METHODS

We sampled seven populations of *Caiman latirostris* (Daudin, 1801) from different sites of Santa Fe Province (Argentina): Costa del Salado (29°42'4.97" S 60°50'37.18" W), Los Amores (28°10'22.75" S 59°59'21.95" W), Palmares (29°44'58.63" S 60°45'55.73" W), Arroyo El Espín (29°58'4.61" S 60°4'57.02" W), Fisco (30°11'47.24" S 61°0'37.65" W), Colonia Mascías (30°48'16.92" S 59°59'5.57" W), and Cacique (30°38'39.72" S 60°16'39.97" W). These sites were chosen to compare them with the previous data obtained by this group (Amavet et al., 2009).

Ten animals from three nests of each sampling site with an average age of four days were randomly selected. The total number of specimens analyzed was 210. Individuals were immobilized by a metal support placed in the neck and were photographed on the dorsal view in the cephalic region using a digital camera SONY Cyber-shot DSC-H20, Full HD 1080, with 10.1 Mp resolution. The camera was placed perpendicular to the center of the cephalic region using a tripod, at a focal distance of about 30 centimeters between the individual and the lens. Furthermore, a graph paper was used as background as metric reference to compute size. From the images 18 landmarks (Lm) were recorded independently three times on the same picture on the cephalic region using the tpsDig2 program (Rohlf, 2004–2007), then all the analyses were performed on the average of the three configurations to reduce the Lm placement error. Procrustes ANOVA was used to measure the error. Procrustes ANOVA is a method for quantifying relative amounts of variation at different levels (Klingenberg and McIntyre, 1998; Klingenberg et al., 2002). Here, this method was used to assess the relative magnitudes of measurement error from repeat measurements.

Furthermore, because the studied structure, i.e., the dorsal view of the skull, presents symmetry, the analysis was performed on the symmetric components, i.e., symmetric landmarks were placed on both sides of the head (Fig. 1).

The choice of the location of Lm was determined considering traditional morphometric measurements of the cephalic region of the caimans (Amavet et al., 2009). The locations of the landmarks used are shown in Figure 1 and their descriptions are in Table 1.

The coordinates of Lm in all specimens were superimposed on a common coordinate system using Generalized Procrustes Analysis (GPA), to remove translation, rotation, and scale effects (Rohlf and Slice, 1999). From the alignment of the specimens, consensus shape was calculated and shape variables were first explored using a Principal Component Analysis (PCA) in each of the populations.

A multivariate regression analysis of Procrustes coordinates was also performed to detect static allometry in populations. In morphometrics, regression is most frequently done to correct for the effects of size on shape (allometry), the residuals from that regression are shape values from which the effects of size have been removed. Thus, the rest of analyzes were performed on the residuals of the regression.

Subsequently, a canonical variates analysis (CVA) was used to visualize shapes and MANOVA (as pairwise comparison) was conducted to determine shape differences between populations, and it was performed first for each of the seven populations and then for all populations together. The CVA was based on the residuals scores of the regression analysis to avoid the size effect.

The relationship between cephalic shape and centroid size over the environmental variables was studied using the partial least squares method (PLS), which is a method used for exploring patterns of covariation between two (and potentially more) blocks of variables. PLS decomposes a *interblock* variance-covariance matrix into mutually orthogonal axes and the

TABLE 1. Location of used landmarks on crocodilian head

Landmark numbers	Description
1	Anterior tip of the snout.
2	Maximum width of the area of the nostrils, right side.
3	Maximum width of the area of the nostrils, left side.
4	Maximum length of the area of the nostrils.
5	Area of right lachrymal.
6	Maximum length of the snout.
7	Area of left lachrymal.
8	Interorbital minimum width, left side (area more convex of left eye).
9	Interorbital minimum width, right side (area more convex of right eye).
10	Maximum length of the area of the right eye.
11	Maximum length of the right eyelid.
12	Maximum length of the area of the left eye.
13	Maximum length of the left eyelid.
14	External corner of flake that cover postfrontal and squamosal bones, left side.
15	Internal corner of flake that cover postfrontal and squamosal bones, left side.
16	Maximum length of the skull.
17	External corner of flake that cover postfrontal and squamosal bones, right side.
18	Internal corner of flake that cover postfrontal and squamosal bones, right side.

components are ordered according to the amount of *covariance* between blocks explained by each one (Zelditch et al., 2004). All the analyses were carried out using the program MorphoJ (Klingenberg, 2011).

The values of environmental variables recorded during the incubation period prior to collection were: medium soil temperature at 10 cm depth (Mst10), precipitation (PP), and relative ambient humidity (RH) and they were kindly provided by the

Instituto Nacional de Tecnología Agropecuaria (INTA). Considering the number of days that nests were exposed to the environment, the averages were calculated from the values of the environmental variables (Table 2).

To examine differences in size in the cephalic region, ANOVA was performed with the centroid size (CS) data, obtained through the MorphoJ programme, of each population.

The heritability of cephalic morphology was calculated for shape (shape distances) and centroid size for the set of seven populations ( $N = 21$  nests), we decided to pool the populations to center the data with a different mean for each of the seven populations, this keeps the variance among nests within population but removes the variance among populations linked to other factors.

To calculate of heritability we used the method of Monteiro et al. (2002), they used a combination of the model of multiple group analysis of variance from Goodall (1991) and the intra-class correlation coefficient (Sokal and Rohlf, 1995) to obtain the different components that contribute to the final calculation of heritability (Eqs. No. 3, 4, and 5 in Monteiro et al., 2002)

The degree of relationship ( $r$ ) among siblings was taken as  $r = 0.50$  for all nests, as it was assumed that individuals were full siblings (see Amavet et al., 2009, 2012). Heritability for each univariate character was calculated as  $h^2 = t/r$  (Falconer and Mackay, 1996).

Collection and handling of animals was corresponding to legal permissions into the framework of Proyecto Yacaré. All animals had been treated following the Ethical Reference Framework for Biomedics Researches: ethical principles for research with laboratory, farm and wild animals (National Scientific and Technical Research Council, 2005), minimising stress and suffering by suitable management methods.

## RESULTS

A principal component analysis captures much of the total shape variance in the first axis (PC 1), which explained between 72% to 83% of the total variance across the seven populations (Table 3). In

TABLE 2. Averaged values of the environmental variables analyzed for each nest

Nest (sample site and number)	Number of days exposed to ambient	Environmental	Variables	
		Medium soil temperature at 10 cm depth (Mst10)-°C	Precipitation (PP)-ml	Relative humidity (RH)-%
Cacique-127	4	22.86	1.04	77.2
Cacique-130	3	22.97	1.15	75.5
Cacique-132	5	22.93	1.77	78.67
Col. Mascías-143	20	23.66	1.13	75.62
Col. Mascías-155	22	23.65	1.67	77.13
Col. Mascías-160	23	23.63	1.64	77.25
C. del Salado-57	17	28.63	1.98	75.72
C. del Salado-172	36	27.85	1.5	75.92
C. del Salado-294	37	27.12	1.29	73.92
Espín-137	22	26.86	1.76	75.95
Espín-140	21	26.69	1.84	75.91
Espín-319	39	26.93	1.68	69.93
Fisco-13	1	29.7	0	70.5
Fisco-73	13	27.88	2.52	77.57
Fisco-102	7	26.71	1.16	73.75
Los Amores-330	37	27.67	3.74	68.88
Los Amores-336	25	27.3	3.98	69.46
Los Amores-344	27	27.23	4.37	69.66
Palmares-237	34	27.58	1.57	75.86
Palmares-247	21	26.43	1.34	76.59
Palmares-300	26	24.82	0.75	71.41

TABLE 3. Eigenvalues and variances explained for each of the populations considering the first two principal components

Population	Principal component	Eigenvalues	% Variance	Cumulative %
Cacique	1	0.00057135	75.838	75.838
	2	0.00005671	7.528	83.366
C. Mascías	1	0.00089128	77.135	77.135
	2	0.00008048	6.965	84.101
C. del Salado	1	0.00148049	82.774	82.774
	2	0.00009409	5.261	88.035
Espín	1	0.00134471	82.827	82.827
	2	0.00007199	4.434	87.262
Fisco	1	0.00073842	72.774	72.774
	2	0.00008449	8.327	81.101
Los Amores	1	0.00105371	80.127	80.127
	2	0.00008243	6.268	86.395
Palmares	1	0.00087355	78.439	78.439
	2	0.00007326	6.579	85.018

all populations, we could observe a shape variation ranging from a longer and wider cranial cavity, with more rounded and smaller eyes, and a shorter snout with a very small nostril region (Fig. 2B-1: Configuration A: configuration on the negative extreme of PC1) which is changing through a continuum toward the positive extreme of the distribution, where we find a configuration with a shorter and narrower head with eyes a little closer together and the snout is longer, sleek, and narrow, with a much larger nostril region (Fig. 2B-2: Configuration B: configuration on the positive extreme of PC1).

Another obvious variation is in the way of insertion from the head to the neck: Configuration A shows a wide region with the landmarks forming an alternant structure along the insertion zone, while Configuration B has a more rounded and elongated posterior region.

The greatest shape difference was observed in the snout: the size of the area of the nostrils (Lm 1 to 4), the length and width of the snout (Lm 1 to 7), the location of the more convex region eyes (Lm 8 and 9), the eye size (Lm 5 to 13), and the length and width of the cranial cavity (Lm 10 to 18). Conversely, there is practically no shape difference in the lacrimal zone (Lm 5 and 7).

In four of the populations analyzed, static allometry was observed in each of the populations separately by the Procrustes ANOVA with a permutation test (10,000 permutation rounds): Cacique:  $P = 0,001$ ; Espín:  $P = 0.0006$ ; Fisco:  $P = 0.0184$ ; and Los Amores:  $P = 0.0135$  and in all populations analyzed combined:  $P = 0.0001$ . The percentage of shape variance explained by size was 10.60%. Because of that, the latter analysis was performed on the residuals of the regression to avoid the static allometry. Moreover, we found that Configuration A corresponds to individuals possessing the smallest total head region and the Configuration B to individuals having the larger total head region (Fig. 3).

The shape of individuals among populations showed differences, the  $P$ -values of the

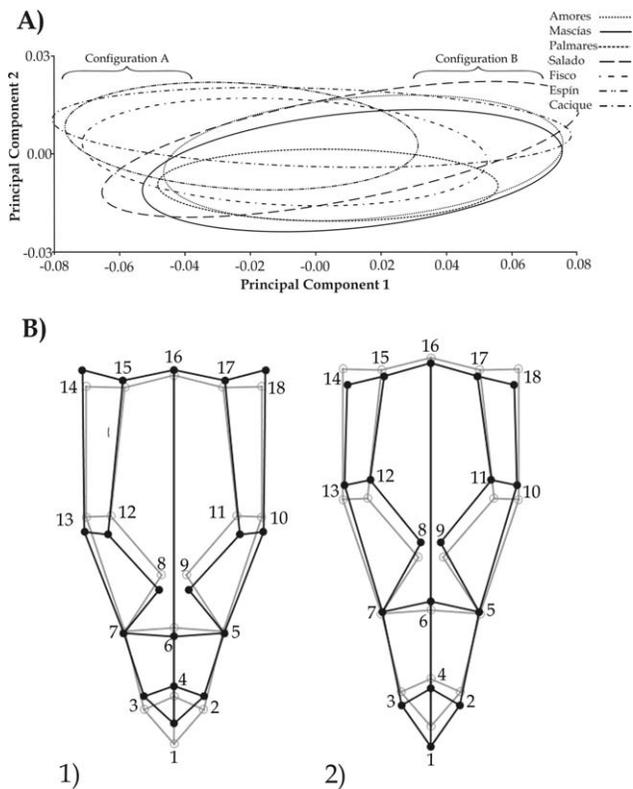


Fig. 2. Ordination plot of the first two principal components. The shape variations in all populations are superposed mainly along the PC1. “Configuration” refers to extreme shapes along PC1 axis. On the negative extreme Configuration A is located while on the positive extreme Configuration B is located. B) Shape variation in dorsal cephalic region. The black line shows the deformation of cephalic shape relative to the gray line that represents the consensus shape. (1) Deformation of cephalic shape relative to consensus shape in the negative scale factor. PC1- Configuration A. The ellipse represent the 95th of confidence. (2) Deformation of cephalic shape relative to consensus shape in the positive scale factor. PC1- Configuration B.

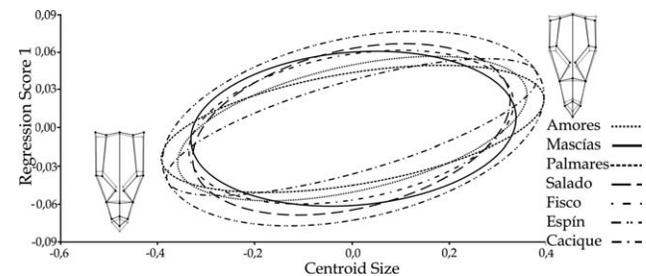


Fig. 3. Allometric relationship between size and shape. The specimens on the left side had the smallest head region (Configuration A), while individuals on the right side had the largest cephalic region (Configuration B). “Regression score” represents the regression coefficients obtained from the regression model of the form with respect to size. The ellipse represent the 95th of confidence.

TABLE 4. Procrustes distances among groups for the set of seven populations

Procrustes distances	P- values						
	Amores	Colonia Mascías	Cacique	Costa del Salado	Espín	Fisco	Palmares
Amores		<b>0,0482</b>	<b>0,0002</b>	0,1063	0,0551	<b>0,0076</b>	<b>0,0156</b>
Colonia Mascías	0,0150		<b>0,0002</b>	0,2177	<b>0,0112</b>	<b>0,0023</b>	<b>0,0413</b>
Cacique	0,0224	0,0276		<b>0,0001</b>	<b>0,0120</b>	0,0819	<b>0,0027</b>
Costa del Salado	0,0134	0,0108	0,0270		<b>0,0427</b>	<b>0,0032</b>	<b>0,0226</b>
Espín	0,0158	0,0215	0,0181	0,0178		0,0815	<b>0,0194</b>
Fisco	0,0193	0,0241	0,0110	0,0237	0,0142		<b>0,0366</b>
Palmares	0,0168	0,0154	0,0176	0,0178	0,0182	0,0145	

P-values from permutation tests (10000 permutation rounds) for Procrustes distances among groups. It was statistically significant for sixteen distances (Procrustes distances are below the diagonal, the  $P$  values are above the diagonal).

permutation test in the Procrustes ANOVA were statistically significant for most Procrustes distances (Table 4). It was observed that the populations more geographically distant differ in shape (Los Amores, Cacique, and Colonia Mascías) in CV1 and CV2 (Fig. 4).

The PLS associations between the Block 1 (cephalic shape) and Block 2 (environmental, geographical, and CS variables) in the set of seven populations (Table 5), were low but we found statistical significance on the relations between shape of all specimens as a whole, and the variables: RV coefficient = 0.029 (Indicates the overall strength of association between blocks);  $P = 0.024$  (10,000 permutations). However, no relation was found between each individual population and these variables (Fig. 5A,B). Particularly, the covariation between cephalic shape (Block 1) and the variables (Block 2) was statistically significant at the PLS 2 (explained 22.74% of the covariation,  $P < 0.0001$ ),

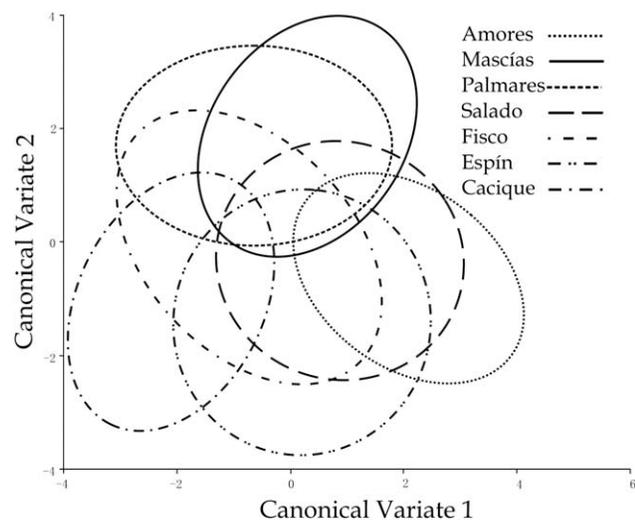


Fig. 4. Canonical Variates Analysis showed the distribution of populations along both canonical axes (CV1 and CV2). The overlapping ellipses shows the populations that have more similarities in the shape of the head region. Los Amores, Cacique, and Colonia Mascías populations presents the ellipses that are more separated and they are the most geographically distant from the other populations. The ellipse represent the 95th of confidence.

and PLS3 (PLS3 explained 10.99% of the covariation,  $P < 0.0001$ ). PLS1 was not significant (explained 60.53% of the covariation,  $P = 0.108$ ). Changes in shape (Block 1) did not show differences among populations in PLS2 and PLS3 (Fig. 5C). The variables (Block 2) in PLS 2 and PLS3, are dominated by CS and RH; and by PP, Longitude and Mst10, respectively, (Fig. 5D). For example, CS defined Los Amores and partially Palmares, populations with larger specimens with respect to the cephalic region. Precipitation defined Colonia Mascías and Cacique populations that are inversely defined by Longitude (which they are located at the East of the distribution together with Los Amores and Espín). Longitude and Mst10 defined Costa del Salado and Fisco, the western populations (Fig. 5D).

The variables most related to cephalic shape, considering the statistical significant PLS, were CS and Longitude and negatively RH in PLS2. Longitude, CS, and Mst10 (directly related to the ambient temperature) were the variables most related in PLS3 (Fig. 5D). Partial least squares analysis reveal that specimens as a whole do not differ in shape, but shape were associated to the variables: environmental, geographical, and CS.

Centroid size was significantly different among populations (ANOVA,  $df = 6$ ,  $df_{res} = 203$ ,  $F = 71.99$ ,  $P < 0.0001$ ) (Fig. 6). The PLS analysis of CS over the environmental variables was statistically significant (PLS1 explained 20.85% of the covariation,  $P < 0.0001$ ).

Heritability value of the cephalic shape was high:  $h^2 = 0.8756$ ; additive genetic variance ( $s_a^2$ ) = 0.0031; and error variance component ( $s_e^2$ ) = 0.004. Concerning the heritability of centroid size (CS), estimated value was also high:  $h^2 = 0.9141$ ; additive genetic variance ( $s_a^2$ ) = 0.0103 and error variance component ( $s_e^2$ ) = 0.0122.

## DISCUSSION

Using geometric morphometrics we found differences in shape and size of the cephalic region between populations of *Caiman latirostris* hatchlings. Shape was also related to environmental

TABLE 5. Partial least squares between blocks showing the covariation and correlation among shape variables (18 landmarks) and environmental and spatial variables in the seven populations as a whole

	Singular value	P-value (perm.)	% total covar.	Correlation	P-value (perm.)
PLS1	0.00712789	0.1088	60.536	0.27095	0.0028
PLS2	0.00436925	0.0001	22.746	0.19640	0.4155
PLS3	0.00303768	0.0001	10.995	0.31904	0.0008
PLS4	0.00167616	0.0001	3.348	0.26461	0.0056
PLS5	0.00126889	0.0001	1.918	0.39165	0.0001
PLS6	0.00061923	0.0001	0.457	0.27733	0.0001

variables for all populations as a whole. Heritability values were high for cephalic shape and size.

Configurations A and B, could be explained as cranial sexual dimorphism, which have been found in most reptilian sauropsids (Bruner et al., 2005; Kaliontzopoulou et al., 2007), and this is probably also the case in the current study, with male individuals displaying Configuration A, and females, Configuration B (Fig. 2). Consistent with this outline, Piña et al. (2007a) suggested that there is

cranial sexual dimorphism in neonates of broad-snouted caiman. The authors concluded that females have a longer skull than males, mainly in the snout region and they suggested that this may be related to the divergence of niches between males and females. Similar results were reported by Fabre et al. (2014) and Herrel et al. (2007), who found sexual dimorphism in the lizards *Tupinambis merianae* and *Anolis carolinensis*, respectively. Both studies agreed that males have more

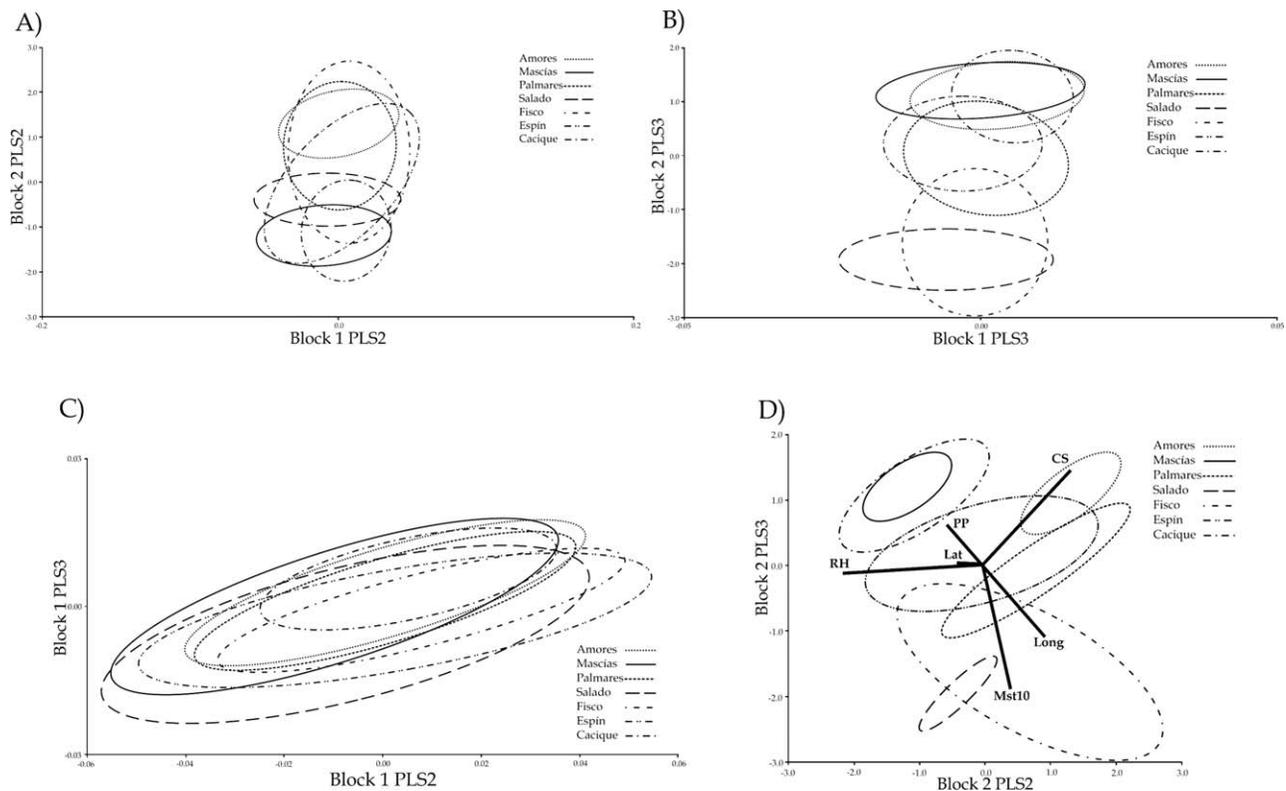


Fig. 5. Partial least squares analysis. **A)** Block 1 PLS2 vs. Block 2 PLS2. The X axis represents changes in cephalic shape in PLS2. The Y axis represents changes in variables (environmental, geographical and CS) in PLS2. **B)** Block 1 PLS3 vs. Block 2 PLS3. The X axis represents changes in cephalic shape in PLS3. The Y axis represents changes in variables (environmental, geographical, and CS) in PLS3. Both graphs shows that PLS3 and PLS2 do not present variation in the cephalic shape in the whole of the seven populations, while there is variation with respect to the variables (environmental, geographical, and CS) in both PLS. **C)** Block 1 PLS 2 vs. Block 1 PLS 3. The X axis represents changes in skull shape in the PLS 2. The Y axis represents changes in cephalic shape in the PLS 3. The ellipses in the graph represents the distribution of individuals of each population corresponding to shape variations. **D)** Block 2 PLS 2 vs. Block 2 PLS 3. The X axis represents the variation of the environmental data in the PLS2. The Y axis represents the variation of the environmental data in the PLS 3. The ellipses in the graph represents the distribution of populations along the Block 2 and the ratio of the distribution with environmental variables (black lines). Mst10: Medium soil temperature at 10 cm depth; PP: Precipitation; RH: relative ambient humidity; Lat: Latitude; Long: Longitude. The ellipse represent the 95th of confidence.

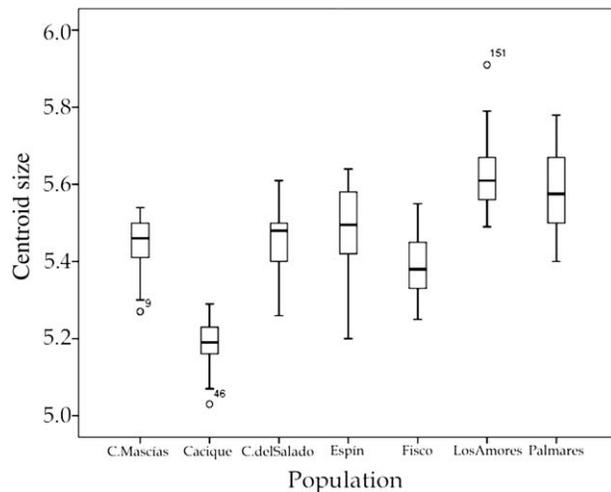


Fig. 6. Distribution of individuals related to their centroid size. It can be seen that Cacique population has the smallest individuals while Los Amores population the largest specimens. The circles represent outliers and numbers identify the individual who owns the outlier.

developed insertion of adductor muscle and relatively shorter rostra than females, causing them to have higher bite forces. These physical characteristics possibly contribute to the difference in diet between males and females. Unfortunately, we could not determine the sex of juveniles of *C. latirostris* studied unless they would have been slaughtered for direct observation of gonads, but this was not possible because the available individuals belong to Proyecto Yacaré.

Based on each particular nesting sites, we observed that specimens shape was not related to variables. However, populations as a whole are related to variables in different ways: as shown in Results, CS and RH, influence the shape of individuals in different ways and therefore in the distribution of some populations in the PLS. The same occur with PP and long.

Many experimental studies on a variety of reptilian sauropsids have shown that important characteristics of the offspring depend on the physical conditions that the embryo experiences prior to hatching (Shine et al., 1997; Qualls and Shine, 1998; Shine and Downes, 1999; Braña and Ji, 2000; Flatt et al., 2001; Warner and Andrews, 2002; Booth, 2006; Warner and Shine, 2007; Piña et al., 2007b; Parachú Marcó et al., 2010). In *Alligator mississippiensis*, Allsteadt and Lang (1995) described that the incubation temperature affected the total size and head size of hatchling and they found a strong nest effect in almost all the characteristics studied. Likewise, Shine et al. (1997), after studying the thermal regimes during incubation period of the lizard *Bassiana duperreyi*, arrived at the same conclusions and also postulate that incubation temperatures induce approxi-

mately half the variation in the phenotype, and the other half is induced by the “origin nest” effect. In our study, we did not detect differences between individuals based on the characteristics of each specific nesting place, but by the environmental characteristics that are shared in particular regions of the sampling area, defined by Latitude (north–south) and Longitude (East–West). That is, those individuals who are located, for example, in the western part of the province were influenced by the geographical characteristics of the region, as detailed below.

Longitude is the factor that exerts a greater influence on the CS of the cephalic region. This can be explained by the fact that the populations are located in the central region of the Province, away from large rivers that cover its eastern boundary (Paraná River basin), with different environmental characteristics (temperature, humidity) to those found in the areas near these bodies of water. The data above are consistent with data of Qualls and Shine (1998) who studied the geographic variation in phenotypic traits of the skink *Lampropholis guichenoti*. The authors measured snout-vent length, inter-limb length, total length, pre-oviposition and post-oviposition mass, and postulated that phenotypic variation is due to direct environmental effects and genetic influence of the population.

Conversely, individuals in a population are similar in shape. This may be due to the variables (environmental, geographical, CS) in each one of the populations are not the main factor that determines the shape of individuals, but there is a strong genetic component that exerts a greater influence. This is consistent with the high heritability value for the shape found. Heritability of shape value in our study is similar to data of Myers et al. (2006), who studied heritability of plastron shape in the turtle *Trachemys scripta*, finding high values for two populations. The authors postulate that the high heritability of plastron shape implies an ability to rapidly respond to selection pressures in a changing environment. This could also be the case of cephalic shape in *C. latirostris*.

The distribution of populations with respect to the centroid size (Fig. 6), demonstrated that the Cacique population showed the smallest cephalic region and, probably, smaller body size than other populations. When environmental data and the records of the eggs harvest campaigns were analyzed, we could conclude two aspects: first, it is one of the populations which was exposed fewer days to the environmental conditions of the place of origin, second, that the registered temperatures in this place were lower, ranging between 22°C and 23°C. Conversely, the populations with longer individuals were Los Amores and Palmares and while analyzing the recorded data, we observed

that eggs were exposed to the natural environment until practically half of embryonic development and local temperatures were high, ranging between 24°C and 28°C. That is, those populations exposed to a greater number of days to the environmental conditions of the place of origin and at higher temperatures resulted in individuals with larger centroid size, and probably larger body size.

With respect to heritability value of centroid size, it was observed that there is high heritability value. This result is in accordance with previous data of our work group (Amavet et al., 2009) where four quantitative body traits in *C. latirostris* hatchlings with high values of heritability were found, including length and weight, indicating that these traits have a good response to directional selection.

In summary, the high heritability values of the shape leads to conclude that cephalic shape of *C. latirostris* hatchlings is mainly influenced by the genetic information underlying ("origin nest effect") which could imply strong response to selection. Conversely, the size also is mainly influenced by the underlying genetic information, but the environmental characteristics also play an important role, apparently, the most influential factor on the size would be the incubation temperature. Studies like this are useful in animal breeding programs: breeders should consider the fact that they can achieve larger sizes in animals in which the artificial incubation conditions eggs are handled after harvest in temperature particularly, as it has been postulated in previous reports in which use traditional morphometry [Booth (2006); Piña et al. (2007b); Parachú Marcó et al. (2010)] Another important issue is to consider the heritability values of centroid size of the animals that are subject to artificial selection pressures to obtain a larger size, since their response will depend on the proportion of genotypic variance the population have.

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