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Allometry of Reproduction in Wild Broad-Snouted Caimans (*Caiman latirostris*)

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ABSTRACT.—We studied 20 nesting female *Caiman latirostris* and their clutches in Santa Fe Province, Argentina. We regressed clutch and egg parameters and hatchling size with several measurements of female size (ln-transformed) to evaluate the allometry of reproduction in the wild. Larger females produced relatively smaller clutches. Larger females produced larger eggs and hatchlings. Egg width, not length, limits egg size relative to female body size. Future studies should address the relationship between female fecundity and hatchling fitness.

The relationship between female body size and clutch size in crocodylians can be related with many aspects of their behavioral ecology and reproductive biology (Peters, 1983). Even though recent investigations have improved our knowledge of crocodylian reproductive biology (see Ferguson, 1985; Thorbjarnarson, 1996), most available information refers to interspecific rather than intraspecific comparisons.

The Broad-Snouted Caiman (*Caiman latirostris*) is the southernmost South American crocodylian reaching to 32°32'S in its geographic distribution (Melo, 2002). The species is considered a valuable natural resource in Argentina (Larriera, 1998) and Brazil (Verdade, 2001a), where conservation and management programs have been stimulating research on many aspects of its biology. However, little information about its reproductive biology is available (Verdade, 1995, 2001b; Piña et al., 2003). The main goal of the present study is to evaluate the allometric relationships between wild reproductive females, and their eggs and clutches. Such information might be useful in the management of the species by determining, for instance, which female body size class contributes most to the annual population reproduction.

MATERIALS AND METHODS

The nesting period of the Broad-Snouted Caiman in Santa Fe, Argentina, extends from late December to mid January. As part of the species management program, eggs are collected in the wild and artificially

incubated (Larriera, 1998). Using pole snares, we captured 20 females, which were assumed to be the actual nest parent based on their protective behavior (Davis et al., 2001). Females were physically restrained and measured to the nearest centimeter in total length (TL) and weighed to the nearest 0.1 kg. Snout-vent length (SVL) values were estimated from total length according to Verdade (2001b). When body mass (BM) was not recorded it was estimated from a pooled sample of both captive and wild animals of similar body size, according to the following regression equation: $BM \text{ (kg)} = -42.7 + 81.41 \text{ SVL (m)}$ ($df = 23$, $F = 107.35$, $P < 0.0001$, $r^2 \text{ adj.} = 82\%$; Verdade, 2003). In the laboratory, we determined clutch size, clutch mass (g), and egg length (mm) and width (mm). In one case we did not measure egg dimensions and in two cases we did not determine clutch mass. Egg volume (mm^3) was then estimated based on the ellipsoid equation $[4/3 \pi (L/2) (W/2)^2]$ as suggested by Wilkinson (1984). Hatchlings were measured with a tape measure to the nearest millimeter and weighed to the nearest 0.1 g with a scale within 24 h after hatching.

We regressed clutch and egg parameters and female body size (ln-transformed; see King, 2000). Observations with a leverage coefficient greater than $4/n$ and high-standardized residuals were excluded and the data reanalyzed (Sokal and Rohlf, 1995). To determine the relationship between clutch size and egg parameters (volume, width, and mass) independent of female body size (BM and TL), we used the residuals of the regression of female body size and egg and clutch parameters.

RESULTS

With the exception of egg length, all other egg and clutch measurements were related to female body size

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TABLE 1. Allometry of reproduction between clutch, eggs and hatchlings, and female body size in the Broad-Snouted Caiman (least-square regression: $y = a + bx$). Relative clutch mass: LN clutch mass (kg)/LN female BM (kg). Egg measurements are presented as clutch average. The column "Number of excluded clutches" presents the data that were excluded from the analysis because high leverage and residual values.

Y	x	a	b	df	F	P	r ² (adj)	Number of excluded clutches
Egg variables								
LN Egg mass (g)	LN Female SVL	4.36	0.88	17	20.06	0.0004	0.53	0
LN Egg length (mm)	LN Female SVL	4.21	0.09	18	1.35	0.2610	0.02	0
LN Egg width (mm)	LN Female SVL	3.79	0.33	17	23.15	0.0002	0.57	1
LN Egg volume (mm ³)	LN Female SVL	11.14	0.74	17	16.11	0.0010	0.47	1
LN Egg mass (g)	LN Female BM	3.18	0.32	16	18.72	0.0006	0.53	1
LN Egg length (mm)	LN Female BM	4.12	0.02	18	0.67	0.4237	<0.01	0
LN Egg width (mm)	LN Female BM	3.41	0.12	17	20.52	0.0003	0.53	1
LN Egg volume (mm ³)	LN Female BM	10.30	0.22	17	12.80	0.0025	0.41	1
Clutch variables								
LN Clutch-size (n)	LN Female SVL	3.76	1.12	19	7.92	0.0115	0.27	0
LN Clutch mass (g)	LN Female SVL	8.11	1.88	17	16.01	0.0010	0.47	0
LN Relative clutch mass (%)	LN Female SVL	2.08	-1.96	16	51.63	<0.0001	0.76	1
LN Clutch-size (n)	LN Female BM	2.42	0.36	19	7.69	0.0125	0.26	0
LN Clutch mass (g)	LN Female BM	5.86	0.59	17	14.52	0.0015	0.44	0
LN Relative clutch mass (%)	LN Female BM	4.14	-0.53	15	57.00	<0.0001	0.79	2
Hatchling variables								
LN Hatchling BM (g)	LN Female SVL	3.86	0.87	12	23.63	0.0005	0.65	1
LN Hatchling TL (cm)	LN Female SVL	3.23	0.38	12	7.94	0.0167	0.37	1
LN Hatchling BM (g)	LN Female BM	2.64	0.33	11	20.41	0.0011	0.64	1
LN Hatchling TL (cm)	LN Female BM	2.76	0.12	13	11.21	0.0058	0.44	0

(SVL and BM; Table 1). All egg, clutch and hatchling measurements were positively correlated with female body size, with the exception of relative clutch mass that presented a negative correlation. Similarly, there was a positive relationship between hatchling and female body size (Table 1). We found no relationship between egg mass or egg volume and clutch size when the effects of female body size were removed (Fig. 1; $P > 0.15$ in all cases).

DISCUSSION

According to Thorbjarnarson (1996) egg size, clutch size, and clutch mass are positively correlated with female body size at the interspecific level in Crocodylians. A similar intraspecific pattern was found for most species examined, with the exception of *C. latirostris* (Thorbjarnarson, 1996). This is contrary to the positive relationship we found (see also Verdade, 2001b). The discrepancy may be caused by the small sample size ($N = 4$) used by Thorbjarnarson (1996). We also found a positive relationship between clutch mass and size and female body size (BM and SVL), similar to the pattern found by Verdade (2001b) for egg size and female body size for the species in captivity. In contrast, Thorbjarnarson (1996) did not find such relationships in *C. latirostris*. Patterns similar to the present results have been reported for *Caiman crocodilus*, *Crocodylus porosus*, *Crocodylus acutus* (Thorbjarnarson, 1996), and *Crocodylus intermedius* (Thorbjarnarson and Hernández, 1993), but not for *Caiman crocodilus* (Thorbjarnarson, 1991).

We found that the relationship of female body size with egg mass is stronger than its relationship with clutch size. A similar pattern has been found in *C. intermedius* (Thorbjarnarson and Hernández, 1993) and *Alligator mississippiensis* (Wilkinson, 1984), but Dietz and Hines (1980) found no relationship in *A. mississippiensis*. Verdade (2001b) found no relationship between clutch size and female body size in *C. latirostris* in captivity.

We did not find a significant relationship between egg size and clutch size, independent of female body size. The same pattern has been described in other crocodylians (Thorbjarnarson and Hernández, 1993; Thorbjarnarson, 1996). However Thorbjarnarson (1994) found a trade-off in egg size and clutch size in *C. crocodilus*.

For the Broad-Snouted Caiman, larger females tended to have larger clutches, and their eggs tended to be heavier and wider but not longer. As in Verdade (2001b), we found that the relationship between female body size and egg width is stronger than with egg length, suggesting that constraints imposed by the pelvic canal may limit egg width (Congdon and Gibbons, 1987). Clutch size in Crocodylians seems to reach its maximum in mature middle-age females but decline in older ones (Joanen and McNease, 1980; Ferguson, 1985). However, egg size appears to increase as female Crocodylians grow older (Ferguson and Joanen, 1983; Hutton, 1984).

Our results suggest that the bigger the female the bigger her hatchlings (see also Verdade 2001b). This pattern can be explained by the relationship between

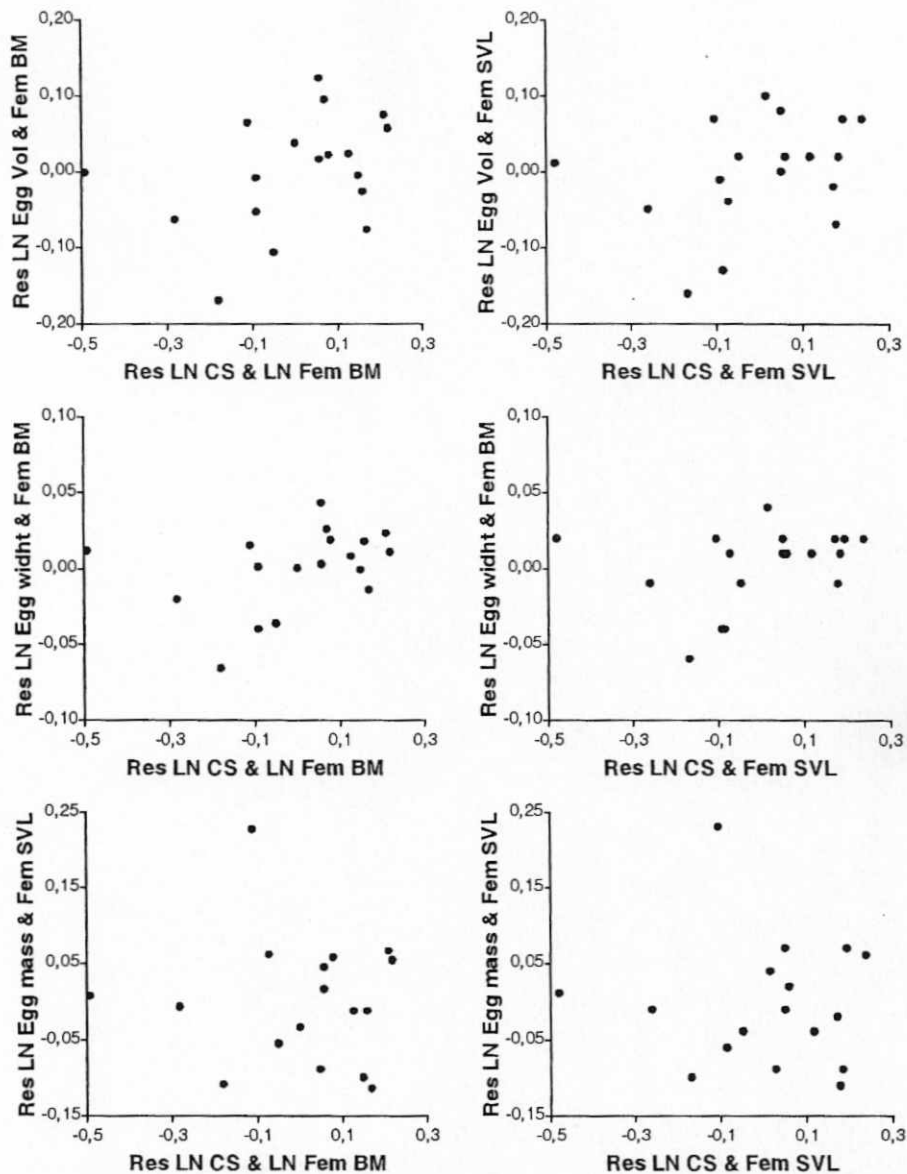


FIG. 1. Plots of residuals of egg measurements and residuals of clutch size independent of female body size.

female body size and egg size, since the larger the egg, the larger the hatchling (Piña et al., 1996).

According to King (2000), if allometric coefficients deviate too much from expected values ($b = 3$ for clutch size and female SVL; or $b = 1$ for clutch size and females BM), it is possible that small and large females employ different reproductive strategies. Our results suggest that small and young reproductive females tend to produce fewer small eggs than middle-aged reproductive females, whereas old mature females tend to produce fewer, larger eggs than middle-age reproductive females. The negative slope in the relationship between female body size and relative clutch mass we found (see also Verdade, 2001b) suggests that larger

females could lay eggs with a higher frequency than smaller females over several nesting seasons because of their relatively smaller energy input (Thorbjarnarson and Hernández, 1993).

Future studies should try to assess fecundity curve and its relationship with hatchling fitness. Such information would be extremely useful in management programs for the species, as well as for the understanding of crocodylian reproductive biology.

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Effect of Incubation Temperature on Incubation Period, Sex Ratio, Hatching Success, and Survivorship in *Caiman latirostris* (Crocodylia, Alligatoridae)

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ABSTRACT.—Temperature-dependent sex-determination has been reported for all extant crocodylians. We present information about incubation temperature effects on incubation period, sex ratio, hatching success, and hatchling survivorship during the first year of life for *Caiman latirostris*. Incubation period was negatively related to temperature. Sex of hatchlings were related to incubation temperature. Only females were produced at 29°C and 31°C, only males were produced at 33°C, and both males and females hatched at 34.5°C. Hatching success and survivorship were unaffected by incubation temperature.

Reptiles have a wide range of sex-determination systems, including genotypic sex determination (GSD) and environmental sex determination (ESD; Wibbles et al., 1994). Temperature-dependent sex determination (TSD), a form of ESD, is present in some turtles

(Ewert et al., 1994) and lizards (Rhen and Crews, 1999), but all crocodylians studied to date (11 of 22 extant species, Lang and Andrews, 1994) show only TSD. It is relevant to know whether temperature is involved in sex determination of all crocodylian taxa because, if all the extant species have TSD, it contrasts with the diversity found in other reptile groups. Moreover, the species studied showed different responses to incubation temperature, for example; *Crocodylus johnstoni* never produced more than 40% males under constant temperature incubation, whereas *Alligator mississippiensis* produced 100% males at certain temperatures (Lang and Andrews, 1994).

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