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Source: Journal of Herpetology, 47(2) : 232-236

Published By: Society for the Study of Amphibians and Reptiles

URL: https://doi.org/10.1670/11-288

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Journal of Herpetology, Vol. 47, No. 2, 232–236, 2013

Reproductive Allometry of *Podocnemis expansa* (Testudines: Podocnemididae) in Southern Brazilian Amazon

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Abstract.—***Podocnemis expansa*** **is the largest freshwater turtle in South America and exhibits a complex reproductive behavior. Females lay eggs in sandy banks formed during the dry season. Nesting habitat can influence hatching success and sex determination. In some turtle species, female body size is crucial to determine reproductive parameters such as clutch size and shape. In this study, we investigate allometric relationships between female body size and their tracks, and clutch characteristics and nest shape in sandy beaches along the Javaés River, southern Brazilian Amazon. Our results indicate that female body size can be estimated based on tracks. Larger females leave larger foot tracks in the sand and have larger clutch sizes with larger clutch mass than smaller females. Female carapace width and body mass can be considered reliable variables to estimate clutch size and total clutch mass for the species. Larger females should be protected because they can be responsible for most annual clutch production.**

Resumo.—***Podocnemis expansa*** **é o maior quelônio de água doce da América do Sul, apresentando um comportamento reprodutivo complexo. Essa espécie nidifica em bancos arenosos formados durante as vazantes dos rios da Amazônia. As características do ambiente de nidificação podem influenciar o sucesso reprodutivo e o sexo dos filhotes. Alguns trabalhos já demonstraram que o tamanho corporal da fêmea é determinante para as condições da ninhada (quantidade e tamanho dos ovos) e nas dimensões dos ninhos (profundidade e diâmetro) em algumas espécies de quelônios. O presente estudo investigou as relações alométricas entre o tamanho corpóreo da fêmea, seus rastros, as variáveis da ninhada e a forma dos ninhos em ambiente natural em uma praia do rio Javaés, na Amazônia Brasileira. Foi observado que o tamanho corpóreo da fêmea de *P. expansa* pode ser estimado em função do seu rastro. Fêmeas maiores deixam rastros maiores na areia, além de produzirem mais ovos (tamanho da ninhada) e com maior massa (massa da ninhada) do que fêmeas menores. A largura da carapaça e a massa da fêmea podem ser consideradas variáveis confiáveis para estimar o tamanho e a massa da ninhada dessa espécie. A proteção de fêmeas de maior tamanho deveria ser priorizada, já que podem ser responsáveis por grande parte da produção anual de ovos.**

Studies of biodiversity are increasingly important because every conservation or sustainable management project requires knowledge of the ecology of the targeted organisms, populations, and ecosystems (Begon et al., 2006). Chelonians are exploited widely throughout the world, and the genus *Podocnemis* is the most highly used group in the Amazon and Orinoco basins (Dupre et al., 2007). As a result, these turtles play an important role in regional economies (Klemens and Thorbjarnarson, 1995). Therefore, information on population and reproductive ecology of this turtle is relevant not only to elucidate its ecology but also for its conservation.

Podocnemis expansa (Schweigger, 1812), Giant Amazon River Turtle, is the largest freshwater turtle in South America (Pritchard, 1979). The species has a complex reproductive behavior that involves nesting on sand banks formed by the reduction of the water level of Amazonian rivers during the dry season. Females store energy for the production of clutches that are oviposited in sand holes (Valenzuela, 2001). We expect that larger females will produce larger clutches in deeper nests.

In most vertebrate species, larger females invest more energy in a clutch than smaller individuals (Reiss, 1991). The tracks that female *P. expansa* leave in the sand after nesting are quite evident and easily measured without disturbing other nesting females (Bonach et al., 2006).

Podocnemis expansa foot tracks have been studied, and the relationship between foot track and female size was suggested but has never been assessed (Valenzuela, 2001; Bonach et al., 2006). In the present study, we investigate the allometric relationships among female body size and track measurements, nest shape, and clutch characteristics of *P. expansa* under natural conditions, providing information for conservation and management practices.

Materials and Methods

Study Area.—Fieldwork was carried out between September and December 2008 on a beach of the Javaés River (09°58′S, 50°05′W), Tocantins state, southern Brazilian Amazon. The local ecosystem is well preserved, and the area is a complex ecotone that includes elements from Cerrado, Amazon Rainforest, and Pantanal (SEPLAN, 2001). The site is located between two important protected areas of the Brazilian Amazon: Parque Nacional do Araguaia and Área de Proteção Ambiental Ilha do Bananal. The climate is tropical wet and dry (Peel et al., 2007), with two well-defined seasons: wet period from November to April (rainy season) and dry period from May to October (dry season). Annual rainfall is approximately 1750 mm and mean annual temperature is approximately 24°C, remaining almost constant throughout the year.

Field Procedures.—Females were captured during three nights at the beginning of the reproductive season (September 2008). During the night (between 0000 and 0600 h), females were located with a spotlight. Researchers waited for females to finish the nesting process to begin morphometric measurements and

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DOI: 10.1670/11-288

TABLE 1. Relationship between foot tracks, clutch, eggs, and female body size in Giant Amazon River Turtle, *Podocnemis expansa* (least-square regression: y = a + bx). BM, body mass; CL, carapace length; CW, carapace width; PW, plastron width; and track 1, foot track on the sand.

y	x	a	b	df	*F*	*P*	r^2 (adj.)	Excluded clutches
Track variables								
Track 1 (cm)	PW (cm)	8.20	1.20	29	16.15	0.0004	0.34	0
Track 1 (cm)	BM (kg)	39.74	0.62	29	23.41	<0.0001	0.44	0
Clutch variables								
Clutch size (*n*)	CL (cm)	−101.98	2.90	29	13.13	0.0011	0.29	0
Clutch size (*n*)	CW (cm)	−56.09	2.63	28	12.29	0.0016	0.29	1
Clutch size (*n*)	BM (kg)	36.62	2.39	29	14.92	0.0006	0.32	0
Clutch size (*n*)	Track 1 (cm)	−15.04	2.07	28	7.07	0.0130	0.18	1
Clutch mass (kg)	CL (cm)	−10.16	0.19	28	39.13	<0.0001	0.58	1
Clutch mass (kg)	CW (cm)	−7.95	0.19	29	46.87	<0.0001	0.61	0
Clutch mass (kg)	BM (kg)	0.06	0.13	29	28.14	<0.0001	0.48	0
Clutch mass (kg)	Track 1 (cm)	−3.07	0.12	28	13.81	0.0009	0.31	1
Egg variables								
Egg mass (g)	CL (cm)	2.02	0.48	29	7.65	0.0099	0.19	0
Egg mass (g)	CW (cm)	−5.93	0.68	28	15.17	0.0006	0.34	1

marking. For each female, we measured carapace length (CL), carapace width (CW), and plastron width (PW) with a metric tape (to the nearest 1 mm) and body mass (BM) with a scale (to the nearest 100 g) according to Malvasio et al. (2005). Turtles were individually marked by drilling and fixing plastic tags to the marginal scutes of carapace (Portelinha, 2010). We measured the tracks left by each female with a metric tape in two ways: 1) foot tracks (track 1) and 2) width of the mark left by the plastron on the sand (track 2) (Bonach et al., 2006). The track measurements were taken on flatter areas of the beach near the nest where the track was straight, and they were clear and firm in the sand. For each track, we took five measurements along the trackway portion and considered the mean value.

Eggs were removed from nests and marked with a pencil to avoid rotation and to ensure return to their original position in the nest (Ewert, 1979; Larriera, 1991). Nonviable eggs (damaged or yolkless) were discarded. Egg length and width measurements were taken with calipers (to the nearest 0.01 mm), and egg mass was measured with a digital scale (to the nearest 0.1 g). Clutch size (total number of eggs in the nest) was recorded, and clutch mass (sum of the mass of each egg) was calculated. These procedures occurred during the period of lower solar intensity (between 0600 and 0900 h or after 1700 h) to avoid death or damage to the embryos because of high temperatures. We measured the following physical characteristics of nests (Bonach et al., 2006): egg-chamber width (width), egg-chamber depth (depth 1), nest height (depth 2), and depth until the first egg on egg chamber (depth 3).

During the incubation period, nests were monitored daily until eggs hatched. Only after hatching were the nests opened again, when the number of unhatched eggs and live and dead hatchlings were counted. We calculated incubation time, hatching success [(number of live hatchlings/clutch size) × 100] and relative clutch mass [(clutch mass/female body mass) × 100]. Measurements of hatchling CL, CW, PW, and BM also were collected.

Statistical Analysis.—We established allometric relationships between female morphometric variables (CL, CW, PW, and BM) and tracks (track 1 and track 2) as predictors (independent variables) of nest (width, depth 1, depth 2, and depth 3), clutch (clutch size, clutch mass, relative clutch mass, and hatching success), egg (egg length, egg width, and egg mass), and hatchling (CL, CW, PW, and BM) variables. Regressions also were established using nest characteristics (width, depth 1, depth 2, and depth 3) as predictors in relation to the clutch variables (clutch size, clutch mass, and hatching success). All variables were tested by linear regression. For regressions between tracks (track 1 and track 2) and female morphometric variables, we used the PW and female BM because these variables are the most representative variables to deduce female body size from a track (Valenzuela, 2001).

We used a Bonferroni correction (Norman and Streiner, 2008) for all predictor variables, considering significant results with $P < 0.025$ for PW; $P < 0.003$ for CL, CW, and BM; and $P < 0.008$ for track 1 and track 2. Observations with leverage coefficient greater than 4/N and highly standardized residuals were excluded and the data reanalyzed (Sokal and Rohlf, 1995). All data were analyzed in the software InfoStat for Windows (INFOSTAT, 2008). Means are reported ± SD.

RESULTS

Thirty *Podocnemis expansa* females were captured during three sample nights in approximately 18 h. We observed that larger (PW) and heavier (BM) females left larger foot tracks in the sand (Table 1). However, no relationship was observed ($P > 0.05$) between track 2 and female morphometric variables (PW and BM).

Nest dimensions (depth and width) were not influenced by female size ($P > 0.05$). However, clutch size and clutch mass were correlated positively to female size (CL, CW, and BM) and track 1. Thus, larger females lay more eggs and produce heavier clutches. We found no relationship between relative clutch mass and female size ($P > 0.05$). Hatching success also was not related to female size ($P > 0.05$). Nest physical characteristics (depth 1, depth 2, or depth 3 and width) were not correlated to clutch size, clutch mass, or hatching success ($P > 0.05$).

Egg mass was related to female carapace length and width (Table 1). However, we observed that egg size (length and width) does not depend on female size ($P > 0.05$). Although bigger females lay more and heavier eggs, there was no relationship between hatchling body size and female morphometric variables (CL, CW, and BM; $P > 0.05$).

Discussion

In turtles, sexual maturity is related to female minimum body size and age (Cagle, 1950; Legler, 1960); for this reason, body length has been used in many studies of reproductive allometry as a basis for relationships (Peters, 1983; Souza et al., 2006). In this study, we used both body size and body mass to establish relationships between nest and clutch variables, tracks, eggs, and hatchlings. The use of other variables, as proposed by this work, may clarify relationships that have not been tested, such as the width of the foot tracks and female body size.

According to Alho and Pádua (1982), *Podocnemis expansa* females reach sexual maturity at a CL of 50 cm. In the present study, female CL = 71.9 ± 4.6 cm (range, 62.0–79.0; $n = 30$). Lower values for adult females of the same species were presented by Cantarelli (2006), with CL = 64.0 ± 3.9 cm (52.5–69.1; $n = 34$). In addition, we observed a mean BM = 29.1 ± 5.8 kg (19.0–41.0; $n = 30$). These values were also greater than those presented by Cantarelli (2006) (24.9 ± 3.1 kg, 17.0–30.0; $n = 34$) for the turtles of the Araguaia River (Goiás state, central Brazil). Although the area studied by Cantarelli (2006) is close to our study site, differences were observed for both CL and BM and could reflect variation between two distinct populations. Generalizations between reproductive status and body size must be made with caution, because there also may be variation due to external factors, such as climate change (Frazer et al., 1993) and hunting pressure (Velasco and Ayarzaguena, 1995), both of which can affect body size at maturity.

We found nest height (depth 2) = 78.9 ± 14.1 cm (46.0–101.0; $n = 30$); however, lower amplitude values were described by Alho et al. (1979) (75.0–80.0 cm), Bonach et al. (2006) (37.5–83.0 cm), and Ferreira Júnior et al. (2007) (53.7–64.8 cm). Variation found by these studies may be related to differences in beach characteristics (such as height and grain size), characteristics that can influence nest digging (Ferreira Júnior and Castro, 2006). No relationship was found between nest depth and hatching success ($P > 0.05$), as described by Bonach et al. (2006). This finding may be related to chelonian embryonic development being more influenced by other nest variables, such as temperature, humidity, and sediment grain size (Morris et al., 1983; Packard et al., 1999; Ferreira Júnior et al., 2007).

Egg-chamber width observed in this study (17.0–52.0 cm; $n = 30$) was higher than values reported by Alho et al. (1979) (20.0–25.0 cm) and Bonach et al. (2006) (16.0–37.5 cm; $n = 10$). The same was observed for depth until the first egg on egg chamber (depth 3) (31.8 ± 5.6 cm, 23.0–46.0; $n = 30$) compared with the studies mentioned above (13.0–18.0 and 10.0–40.0 cm, respectively). Some studies suggested that nest dimensions are related to female body size, because smallest females should have limitations to dig wider and deeper nests (Ehrhart, 1995; Valenzuela, 2001; Morjan, 2003; Bonach et al., 2006). However, no relationships ($P > 0.05$) were found between nest dimensions (depth 1, depth 2, or depth 3 and width) and female body size (CL, CW, and BM) or foot track (track 1), suggesting larger and smaller females may dig similar nests in some areas.

Foot tracks varied from 47.0 to 67.0 cm (57.7 ± 5.8 cm; $n = 30$), and the mark of female plastron in the sand varied from 15.0 to 26.0 cm (20.4 ± 5.3 cm; $n = 30$). Similar values for tracks have been presented by Valenzuela (2001) (54.8 ± 4.3 cm, 44.0–66.0 cm for foot tracks; $n = 88$) and Bonach et al. (2006) (50.4 ± 3.6 cm, 43.0–55.5 cm for foot tracks and 21.9 ± 2.5 cm, 18.5–26.5 cm for Ttrack 2; $n = 14$). We found a positive relationship between foot tracks, female body size, and clutch size, suggesting that trackways are useful to relate these variables as it has been hypothesized for this species (Valenzuela, 2001; Bonach et al., 2006). However, because the type of sediment could affect these relationships, extrapolation to other sites should be taken with caution.

Furthermore, we found a strong relationship between clutch size and clutch mass and all female morphometric variables, including foot tracks (Table 1). This relationship demonstrates that larger females tend to produce larger clutches with heavier eggs, as it has been observed for the Amazonian species *Podocnemis sextuberculata* (Haller and Rodrigues, 2006) and some species of crocodilians (Thorbjarnarson, 1996; Verdade, 2001; Larriera et al., 2004). However, although the generated model explained more than 60% of variation for some relationships (Table 1), other factors, such as population density, nutritional status, age, and climate variables, should be considered in studies with reptiles because they may influence clutch size and clutch mass (James and Whitford, 1994).

Podocnemis expansa produces large clutches. Soares (1996) and Bonach et al. (2006) found similar clutch sizes for this species in different locations in the Brazilian Amazon (105.0 and 103.0 ± 18.2 eggs, respectively). Hildebrand et al. (1988) observed a mean clutch size of 105.0 eggs for the *P. expansa* population of the Caquetá River (Colombia), and a similar value was reported by Valenzuela (2001) (103.0 ± 23.7 eggs). Iverson et al. (1993) suggested that variation in clutch size of a particular species may be associated with latitudinal differences, as observed in *Clemmys guttata* (Litzgus and Mousseau, 2006) and crocodilians (Wilkinson, 1983; Simoncini et al., 2009). The mean clutch size found in this study (106.0 ± 23.6 eggs, 36.0–141.0; $n = 30$) is similar to values reported for different populations of this species in different regions of the Amazon, regardless of latitudinal variation (0–13°S; 09°S in our study). Although clutch size is similar in these areas, female size seems to be different (e.g., CL = 74.1 ± 4.2 cm [Soares, 1996]; CL = 64.0 ± 3.9 [Cantarelli, 2006]; and CL = 71.9 ± 4.6 cm [this study]). This observation should not be expected if the relationship between female size and clutch size found in this study is the same in all these areas. Future studies should investigate this question.

Our results suggest that, as adult *P. expansa* females increase their size, they also store more energy (in absolute terms) for reproduction, as suggested by the increase in clutch mass with the female body size (Table 1). Moreover, our data indicate that larger females invest in the production of not only more eggs but also heavier eggs, as described by Valenzuela (2001). Nevertheless, we found no relationships between body size and relative clutch mass. This finding indicates that there is no difference in the relative energetic investment among females from different size classes (or ages), contrary to what was observed by Cantarelli (2006) for *P. expansa* and in some crocodilians species (Thorbjarnarson and Hernández, 1993; Verdade, 2001; Larriera et al., 2004).

Egg dimensions (length, width, and mass) found in this study (41.3 ± 1.5 mm, 38.8 ± 1.6 mm, and 36.4 ± 4.7 g, respectively) were smaller than those observed by Ojasti (1971) (46.0 mm, 40.0 mm, and 40.0 g) in the Orinoco River (Venezuela). Although latitudinal variation did not affect clutch size (as described herein), we may not discard the possibility that egg size could be influenced by this factor, as proposed by Vanzolini (1997).

The possibility of establishing relationships between foot tracks, size and number of eggs and hatchlings, and physical nest characteristics and nesting female will contribute positively to management techniques of *P. expansa* conservation programs in situ and ex situ, making the estimation of number of eggs per beach easier, allowing to prioritize the protection of the most productive clutches (based on clutch size), and clarifying the reproductive potential of each individual (e.g., the curve of population fertility; Begon and Mortimer, 1996). Moreover, such information may improve future management plans for this species by allowing for the prioritization of conservation of large females. In addition, environmental education programs should emphasize to the local populations (riverine and indigenous) the importance of protecting these individuals and avoiding the removal of large, reproductive *P. expansa* females. These methods can be used as field tools in conservation and management programs being of simple application, because they are easier than measuring live animals, generate less stress (handling of the animals is not required), incur low costs, and can provide estimates of clutch size at nesting beaches.

Acknowledgments.—We are grateful to Universidade Federal do Tocantins (UFT), Centro Nacional de Pesquisa e Conservação de Répteis e Anfíbios do Instituto Chico Mendes de Conservação da Biodiversidade (RAN/ICMBio), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; process 482584/2007-6) for the logistical and financial support during the fieldwork. TCGP received a master's scholarship from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP; process 2007/05040-0), and AM and JB had grants from CNPq (processes 503650/2009-9 and 305868/2009-8). We thank L. M. Verdade and T. Rainwater for review, suggestions, and encouragement. The indispensable support of the research group Crocodilianos e Quelônios da Região Norte (CROQUE-UFT), especially to KMM and the staff of Centro de Pesquisas Canguçu (Josilene, Roberto, and Sulene), was crucial to this work. All field procedures were authorized by Brazilian Federal Environmental Agency (IBAMA/ICMBio, permit 16514-1). We also thank three anonymous reviewers who contributed significantly to the improvement of the manuscript.

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Accepted: 6 March 2012.