Série Zoologia

Iheringia

e-ISSN 1678-4766 www.scielo.br/isz

Article



Sexual dimorphism and morphometrics in two populations of the Neotropical freshwater turtle *Mesoclemmys vanderhaegei* (Testudines, Chelidae)

Elizângela S. Brito^{1,2} (b), Richard C. Vogt^{3†} (b), Rosa Helena S. Ferraz⁴ (b), Christine Strüssmann⁴ (b), Rafael M. Valadão⁵ (b) & Izaias M. Fernandes⁶ (b)

- 1. Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo, 2936, Petrópolis, 69067-375 Manaus, AM, Brazil. (eliz.chelidae@gmail.com)
- 2. Programa de Pós-graduação em Ciências Veterinárias, Universidade Federal do Mato Grosso, Av. Fernando Correa da Costa, 2367, Boa Esperança, 78060-900 Cuiabá, MT, Brazil.
- 3. Coordenação de Biodiversidade, Centro de Estudos dos Quelônios da Amazônia, Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo, 2936, Petrópolis, 69067-375 Manaus, AM, Brazil.

 Faculdade de Medicina Veterinária, Universidade Federal de Mato Grosso, Av. Fernando Correa da Costa, 2367, Boa Esperança, 78060-900 Cuiabá, MT, Brazil.
Centro Nacional de Pesquisa e Conservação de Répteis e Anfíbios, Instituto Chico Mendes de Conservação da Biodiversidade, Rua 229, 95, Setor Leste Universitário, 78605-090 Goiânia, GO, Brazil.

6. Universidade Federal de Rondônia, Campus Universitário Rolim de Moura, Av. Norte Sul, 7300, Nova Morada, 76940-000, Rolim de Moura, RO, Brazil. † Deceased.

Received 29 January 2021 Accepted 6 January 2022 Published 25 February 2022

DOI 10.1590/1678-4766e2022004

ABSTRACT. As commonly observed in turtles, sexual size dimorphism (SSD) is pronounced in the Neotropical freshwater turtle *Mesoclemmys* vanderhaegei (Bour, 1973), a species in which females are usually larger than males. We studied SSD in two populations of *M. vanderhaegei* from the Brazilian Cerrado savannah, based on 245 specimens captured between November 2010 and August 2013. The carapace length of the largest male was 201 mm (9.15% shorter than that of the largest female, 220 mm). The mean sizes of males and females did not differ in the two populations. However, a comparison of eight selected morphological variables revealed that the size distribution pattern differed between the populations. Using model selection, seven out of 34 morphometric variables – from the head, plastron, bridge, and tail – were selected as the most suitable ones to distinguish between males and females. The pattern of SSD found in *M. vanderhaegei* is similar to that found in other chelonian species and may be the result of natural selection rather than ecological factors, since individuals of both sexes use the same habitats.

KEYWORDS. Sexual size dimorphism, Cerrado, body size, model selection.

RESUMO. Dimorfismo sexual e morfometria em duas populações do quelônio aquático Neotropical *Mesoclemmys vanderhaegei* (Testudines, Chelidae). Como comumente observado em quelônios, dimorfismo sexual em tamanho (SSD) é pronunciado em *Mesoclemmys vanderhaegei* (Bour, 1973), uma espécie de quelônio Neotropical de água doce onde as fêmeas são geralmente maiores que os machos. Nós estudamos SSD em duas populações de *M. vanderhaegei* no Cerrado brasileiro, com base em 245 espécimes capturados entre novembro de 2010 e agosto de 2013. O comprimento da carapaça do maior macho foi de 2011 mm (9,15% menor que o comprimento da maior fêmea, 220 mm). Os tamanhos médios de fêmeas e machos não diferiram nas duas populações. No entanto, uma comparação de oito variáveis morfológicas revelou que o padrão de distribuição de tamanhos diferiu entre as populações. Usando a seleção de modelos, sete das 34 variáveis morfométricas – incluindo medidas da cabeça, plastrão, ponte e cauda – foram selecionadas como as mais adequadas para distinguir fêmeas e machos. O padrão de SSD encontrado em *M. vanderhaegei* é similar ao encontrado em outras espécies de quelônios e pode ser o resultado de seleção natural ao invés de fatores ecológicos, uma vez que indivíduos de ambos os sexos usam os mesmos habitats.

PALAVRAS-CHAVE. Dimorfismo sexual em tamanho, Cerrado, tamanho do corpo, seleção de modelos.

Many theories have been proposed to explain sexual dimorphism, such as the theory of reproductive effort, which assumes that females are larger than males because of reproductive issues (RALLS, 1976; SCHOENER *et al.*, 1982); the niche partitioning theory, which assumes that dimorphism is greater in populations where competition for food is more intense (SCHOENER, 1967, 1968); the competition theory, which presumes that dimorphism is greater in populations with fewer competitors (SCHOENER, 1977); the theory of island size, which suggests a correlation between the mass/size of males and females and their home ranges (IVERSON,

1984), and finally, the geographical distribution theory, which suggests that sexual dimorphism may vary throughout the geographical distribution, in widely distributed species (FITCH, 1981; IVERSON, 1984; see also LOVICH *et al.*, 1998). Thus, sexual dimorphism may be related both to ecological differences (e.g., behavioural traits, feeding habits, and differentiated use of habitat between sexes) and to differences in the body size of males and females (BERRY & SHINE, 1980; SHINE, 1989) – sexual size dimorphism (SSD). Chelonians often exhibit sexual size differences (BERRY & SHINE, 1980). These differences can be explained by the theory of sexual

selection, based on aspects related to fighting between males, and especially, selection of males by females, which is quite marked among chelonians (BERRY & SHINE, 1980). Males are larger in species of chelonians that present fighting or forcible insemination and are smaller in species where these traits are absent (BERRY & SHINE, 1980).

Morphometric peculiarities in chelonian females (BONNET *et al.*, 2001) include, for example, a larger circumference of the abdominal region to produce larger or more numerous eggs (GIBBONS *et al.*, 1982). These larger females may be selected by males because of their ability to produce more offspring (FORSMAN & SHINE, 1995). On the other hand, morphological and morphometric specificities of males may be related to mobility, since they travel over long distances in their search for females to mate with. In this case, they are expected to be smaller in size and to have more developed musculature than females (BONNET *et al.*, 2001).

Mesoclemmys vanderhaegei (Bour, 1973) is a spec ies of freshwater turtle widely distributed in South America, which has been reported in the Amazon, São Francisco, Tocantins, and La Plata river basins (see VINKE et al., 2013; MARQUES et al., 2014). Data on the species' population ecology were so far obtained from four populations, in Southeast (MARQUES et al., 2013) and Central Brazil (BRITO et al., 2009, 2018). Females are larger than males in all these populations. However, no one has discussed which morphological traits in particular can be responsible for such differences. This information is necessary because carapace length alone does not reliably indicate the sex of the individuals, as some size ranges include both genders (READEL et al., 2008). Currently, distinguishing the sex in individuals of the species is usually performed by measuring the precloacal tail length, which is longer in males than in females (BRITO et al., 2016, 2018), as alternative methods such as penile eversion do not work for sexing M. vanderhaegei (RODRIGUES et al., 2014; MCKNIGHT et al., 2017).

In this study, multivariate statistics and the model selection approach were used to ascertain: 1) whether there are morphological differences between males and females – besides carapace length – in two Brazilian populations of *Mesoclemmys vanderhaegei*; 2) whether the eight morphometric variables commonly used in studies of chelonians are effective for sexing individuals, and 3) whether the best model that describes sexual dimorphism in the species, based on 34 morphometric variables, includes the eight variables normally used for this purpose.

MATERIALS AND METHODS

Study area. The data were collected in two protected areas situated in the state of Mato Grosso, midwestern Brazil: Estação Ecológica Serra das Araras (EESA), in the municipalities of Porto Estrela and Cáceres (15°46'09"S; 57°13'10"W; datum: WGS84; between 537m and 774m a.s.l.), and Parque Nacional da Chapada dos Guimarães (PNCG), in the municipality of Chapada dos Guimarães (15°24'59"S; 55°50'29"W; datum: WGS84; 604m a.s.l.).

The two conservation units are about 180 km apart. Three small streams in EESA and five in PNCG were selected for the study. The sampled streams are perennial, small, shallow, nutrient poor, slightly acidic, with low electrical conductivity, and are shaded and protected by dense gallery forest (RIBEIRO & WALTER, 2001; FONSECA, 2005), except nearby springs located amidst sparse grassland. For additional details on the habitats usually occupied by *Mesoclemmys vanderhaegei*, see descriptions and images in VINKE *et al.* (2013) and MARQUES *et al.* (2014).

Experimental design. We collected data between November 2010 and August 2013, during nine sampling sessions at each site (EESA: November 2010; June, September, and November 2012; April, June, August, and November 2012; May 2013; PNCG: December 2010; April and September 2011; May, September, and November 2012; April, June, and August 2013). *Mesoclemmys vanderhaegei* were caught in baited funnel traps 1.2 m in length (BRITO *et al.*, 2009), baited with a mixture of beef and fish-flavored cat food. For each sampling, we installed traps on the margins or in the center of each stream. In all streams, we operated the traps continuously for six 24-h periods and checked them once a day, early in the morning. We sampled each site for a total of 54 d (6 d × nine samples). Our sampling effort totalled 21,600 trap-hours.

Each captured individual was marked using the marking method adapted from CAGLE (1939), which consists of a combination of notches and removal of rectangular pieces from the marginal scutes of the carapace. The sex of the individuals was determined *a priori* by means of secondary sexual characteristics – males have longer tails than females, represented by the morphometric variables PCL and TL (see Fig. 1). Individuals with a carapace length (CL) of less than 115 mm – which could not be sexed –were classified as juveniles. The categories of "male" and "female" may comprise both adult and sub-adult individuals, since we do not know the age and/or size of *M. vanderhaegei* at sexual maturation.

Eight morphometric variables (in mm) were measured in all individuals (N = 245) (see Tab. I). In addition to these widely used measurements (see below, in "Statistical analyses"), 26 other variables were obtained from a random subsample of 64 individuals of known sex, positively identified as either males or females (Fig. 1; Tab. I). Most of these morphometric variables originate from a combination of head, carapace, plastron, and tail measurements, and are based on standard measurements used in previous studies with freshwater turtles, while others are being used here for the first time (see Tab. I).

All the morphometric measurements were linear, taken to the nearest 0.05 mm using a 300 mm stainless steel manual calliper. Body mass was weighed using spring scales with the following capacities: 100 g (0.1 g precision), 1,000 g (1.0 g precision), and 5,000 g (50 g precision). After being measured and marked, the turtles were released at their capture sites.



Fig. 1. Measured morphometric variables of the individuals of *Mesoclemmys vanderhaegei* (Bour, 1973). Head: Head width (HW); Head length (HL); Interorbital width (IOW); Tympanum-snout length (TSL); Tympanum length (TYL); Tympanum width (TW). Carapace: Nuchal scute length (NL); Carapace length (CL); Maximum carapace width (MCW); Central carapace width (CCW); Length of third central scute (LC3); Width of third central scute (WC3). Shell: Maximum carapace height (MHS). Plastron: Maximum plastron length (MPL); Mid-ventral suture length plastron (MVSL); Maximum plastron width (MPW); Anterior lobe width (ALW); Posterior lobe width (PLW); Width of left and right gular scutes (WGS); Length of left gular scute (LGS); Left gular scute length (GSL); Intergular scute width (IG); Left pectoral scute width (PSW); Left pectoral scute length (MBL2); Left abdominal scute length (ASL); Left abdominal scute width (ASW); Maximum bridge length (MBL); Minimum bridge length (MBL2); Left anal scute width (ANSW); Left anal scute length (ANSL); Internal diagonal of anal scute (IDS); Carapace anal plastron terminal distance (CPD). Tail: Precloacal length (PCL); Tail length (TL).

Tab. I. I	Morphometric variable	s obtained from 245	individuals of A	Aesoclemmys v	anderhaegei (Bour,	1973) (eight v	variables; indicated	by *) and	l, among
these, f	rom 64 individuals iden	ntified as either male	es and females (26 additional v	ariables; indicated b	oy **).			

Variables – abbreviation	References
Head width – HW*	McCord <i>et al.</i> (2001), Bour & Zaher (2005)
Head length – HL**	McCord <i>et al.</i> (2001)
Interorbital width - IOW**	McCord <i>et al.</i> (2001)
Tympanum-snout length – TSL**	This study
Tympanum length – TYL**	This study
Tympanum width – TW**	This study
Nuchal scute length – NL**	BAGER et al. (2010, 2016)
Carapace length – CL*	McCord et al. (2001), Bour & Zaher (2005), Bager et al. (2010, 2016)
Maximum carapace width - MCW*	McCord et al. (2001), Bour & Zaher (2005), Bager et al. (2010, 2016)
Central carapace width - CCW**	BAGER et al. (2010, 2016)
Length of third central scute – LC3**	BAGER et al. (2010, 2016)
Width of third central scute - WC3**	BAGER et al. (2010, 2016)
Maximum carapace height - MHS*	McCord et al. (2001), Bour & Zaher (2005), Bager et al. (2010, 2016)
Maximum plastron length - MPL*	McCord et al. (2001), Bour & Zaher (2005), Bager et al. (2010, 2016)
Mid-ventral suture length plastron - MVSL**	McCord et al. (2001), BAGER et al. (2010, 2016)
Maximum plastron width - MPW*	McCord et al. (2001), Bour & Zaher (2005), Bager et al. (2010, 2016)
Anterior lobe width – ALW**	McCord et al. (2001), Bour & Zaher (2005), Bager et al. (2010)
Posterior lobe width – PLW**	McCord et al. (2001), Bour & Zaher (2005), Bager et al. (2010, 2016)
Width of left and right gular scutes - WGS**	BAGER et al. (2010, 2016)
Length of left gular scute – LGS**	BAGER <i>et al.</i> (2016)
Left gular scute length – GSL**	BAGER et al. (2010, 2016)
Intergular scute width – IG**	McCord et al. (2001), Molina et al. (2012)
Left pectoral scute width - PSW**	BAGER <i>et al.</i> (2010)
Left pectoral scute length – PEL**	BAGER et al. (2010, 2016)
Left abdominal scute length - ASL**	BAGER <i>et al.</i> (2010)
Left abdominal scute width - ASW**	BAGER et al. (2010, 2016)
Maximum bridge length - MBL**	McCord et al. (2001), BAGER et al. (2010, 2016)
Minimum bridge length - MBL2**	Bour & Zaher (2005)
Left anal scute width - ANSW**	BAGER <i>et al.</i> (2016)
Left anal scute length – ANSL**	BAGER et al. (2010, 2016)
Internal diagonal of anal scute - IDS**	This study
Carapace anal plastron terminal distance - CPD**	BAGER et al. (2010, 2016)
Precloacal length – PCL*	Dustman (2013)
Tail length - TL*	Ernst (1971)

Statistical analyses. We used the non-parametric multivariate analysis of variance (NP-MANOVA; ANDERSON, 2001) to determine whether the eight variables commonly measured in chelonians (CL, HW, MCW, MHS, MPL, MPW, PCL, and TL; Tab. I) differ between males and females from the two populations of *M. vanderhaegei*. It was implemented using the adonis function of the Vegan package (OKSANEN *et al.*, 2012).

To determine which of the 34 measured morphometric variables best explain the SSD in *Mesoclemmys vanderhaegei* we only used the data obtained from 64 individuals of known sex, with CL between 115 and 196 mm (Tab. I). We

transformed sex into a binary variable and standardized all measurements according to the CL. We then used multimodels to find the combination of variables that best explains the morphological differences between the sexes, eliminating correlated variables, based on the glmulti package (CALCAGNO & MAZANCOURT, 2010). The models were classified by the Akaike Information Criterion (AIC), which clarifies uncertainties about the set of candidate models (BURNHAM & ANDERSON, 2002), and by the Δ AIC values, where the lowest values indicate the best models. We considered that all the models with Δ AIC<2 were equally good, but here we considered only the best model (lowest Δ AIC). The variables of the best model selected based on the AIC were used in a non-parametric multivariate analysis of variance (NP-MANOVA, ANDERSON, 2001) to determine whether males and females really differ according to the morphological variables selected by the best model. We then performed a Principal Component Analysis (PCA) and extracted the first and second axes, using a broken-stick selection criterion (JACKSON, 1993) to obtain a visual representation that would enable males and females to be distinguished with respect to the variables tested by NP-MANOVA. We used a Pearson's correlation to determine which morphological variables were related to axes generated by the PCA. All the statistical analyses were performed using the R program (R DEVELOPMENT CORE TEAM, 2016), at a significance level of 0.05.

RESULTS

We measured 245 individuals of *Mesoclemmys* vanderhaegei during the study. Fifty-eight of these individuals were captured at the Parque Nacional da Chapada dos Guimarães (PNCG; 31 males, 27 females) and 187 were captured at Estação Ecológica Serra das Araras (EESA; 74 males; 113 females). The females presented a significantly longer CL than males in the two sampled areas (PNCG t = 2.41; p = 0.01 – EESA t = 4.25; p < 0.01). Females reached a maximum CL of 220 mm, with a mean length of 157.80±32.30 mm in PNCG and 155.60±20.37 mm in EESA; the difference in CL between the females of the two sites was negligible ($F_{1.59} = 0.09$; p = 0,76). The largest male captured in EESA had a CL of 201.30 mm, 9.15% smaller than the largest female captured. The mean CL of

males was 139.45 \pm 7.50 mm in PNCG and 142.50 \pm 11.07 mm in EESA; the difference in CL between the males of the two sites was negligible (F_{1.52} = 0.35; p = 0.56).

The set of eight variables normally evaluated in studies of morphometric aspects of chelonians enables males to be distinguished from females in the two populations under study (PNCG – NP-MANOVA: $F_{1,58} = 8.24$, $R^2=0.12$, p < 0.002; EESA – NP-MANOVA: $F_{1,187} = 15.99$, $R^2=0.07$, p < 0.001). The differences in the size of males and females are more noticeable in PNCG (Fig. 2) and less marked in EESA (Fig. 3). The first and second axes of the PCA captured a large part of the variation in the morphometric data, with 90.9% corresponding to PNCG and 81.7% to EESA.

Using the 34 morphometric variables measured in 64 sexed and randomly chosen individuals from the two populations, we generated 610 models that describe the sexual dimorphism in Mesoclemmys vanderhaegei. Fortysix of these models were within two units of \triangle AIC and 72 reached 95% of the total weight of the models. The best model selected seven morphometric variables to differ between males and females, namely, maximum plastron length (MPL) + mid-ventral suture length (MVSL) + maximum bridge length (MBL) + posterior lobe width (PLW) + precloacal length (PCL) + tympanum-snout length (TSL) + tympanum length (TYL). The best model presented AIC of 45.50 and Wi-AIC of 0.003. The variables selected by the best model indicate that the morphometric traits of males and females differ significantly (NP-MANOVA: $F_{1.63} = 20.4$, R²=0.24, p = 0.006). The first and second axis of the PCA captured much of the data variance, accounting for 75.09% of the total variation. Based on the variables selected by the best model, we observed evident sexual dimorphism (Fig. 4; Tab. II).



Fig. 2. Multidimensional distribution of females (F) and males (M) of *Mesoclemmys vanderhaegei* (Bour, 1973), using eight morphometric variables commonly measured in chelonians in Parque Nacional da Chapada dos Guimarães (PNCG), Brazil.



Fig. 3. Multidimensional distribution of females (F) and males (M) of *Mesoclemmys vanderhaegei* (Bour, 1973), using eight morphometric variables commonly measured in chelonians in Estação Ecológica Serra das Araras (EESA), Brazil.



Fig. 4. Multidimensional distribution of females (F) and males (M) of *Mesoclemmys vanderhaegei* (Bour, 1973), using the seven variables selected by the best model. In this ranking we present information about 64 sexed individuals captured in Parque Nacional da Chapada dos Guimarães (PNCG) and in Estação Ecológica Serra das Araras (EESA), Brazil.

Among the eight morphometric variables commonly used in chelonians (CL, HW, MCW, MHS, MPL, MPW, PCL, and TL; body mass excluded), only two – MPL and PCL – were selected by the best model and three – MCW, MHS, and TL – were selected by the 46 models with Δ AIC<2. Three other variables – CL HW, and MPW – do not allow one to distinguish between *Mesoclemmys vanderhaegei* males and

females. Another 22 morphometric variables, among the 34 analyzed, were selected by the 46 models with $\Delta AIC < 2$: IG, TL, LGS, PSW, WC3, ANSL, PEL, HL, ALW, ANSW, NL, LC3, ASW, MBL2, ASL, MHS, IDS, TW, WGS, CPD, MCW, and GSL. Of the 34 morphometric variables measured, only five (CL, CCW, HW, IOW, and MPW) were not selected by the best model or by the 46 models with $\Delta AIC < 2$.

Tab. II. Results of Pearson's correlation between the axes of the PCA generated by the seven variables selected by the best model for the two populations of *Mesoclemmys vanderhaegei* (Bour, 1973) treated herein, from Parque Nacional da Chapada dos Guimarães (PNCG) and Estação Ecológica Serra das Araras (EESA), Brazil.

	PNCG			EESA				Best Model				
Variables	PCA1		PCA2		PCA1		PCA2		PCA1		PCA2	
	r	р	r	р	r	р	r	р	r	р	r	р
LC	-0.98	<0.001	0.10	0.41	-0.97	<0.001	0.03	0.61	-	-	-	-
MCW	-0.96	<0.001	0.17	0.19	-0.95	<0.001	0.09	0.17	-	-	-	-
MPL	-0.96	<0.001	0.21	0.10	-0.97	<0.001	0.04	0.51	-0.18	0.14	0.15	0.21
MPW	-0.96	<0.001	0.17	0.17	-0.95	<0.001	0.12	0.09	-	-	-	-
MHS	-0.04	<0.001	0.09	0.47	-0.93	<0.001	-0.05	0.42	-	-	-	-
PCL	-0.53	<0.001	-0.76	<0.001	-0.21	0.002	-0.87	<0.001	0.96	<0.001	-0.80	<0.001
TL	-0.77	<0.001	-0.06	0.62	-0.61	<0.001	-0.50	<0.001	-	-	-	-
HW	-0.96	<0.001	0.14	0.27	-0.94	<0.001	0.16	0.02	-	-	-	-
MVSL	-	-	-	-	-	-	-	-	-0.33	0.006	0.01	0.91
MBL	-	-	-	-	-	-	-	-	-0.33	0.006	0.33	0.007
PLW	-	-	-	-	-	-	-	-	-0.33	0.007	0.29	0.01
TSL	-	-	-	-	-	-	-	-	-0.10	0.42	0.16	0.19
TYL	-	-	-	-	-	-	-	-	0.12	0.33	0.11	0.37

DISCUSSION

The Mesoclemmys vanderhaegei populations studied show marked sexual dimorphism (SSD), with females being larger than males, as has already been observed in other populations from this species (BRITO et al., 2009, 2018; MARQUES et al., 2013; 2014). This is an attribute common, also, among other species of Chelidae (RHODIN et al., 1984; MOLINA, 1998; BAGER et al., 2016; GARBIN et al., 2016) and other families of aquatic turtles (BERRY & SHINE, 1980). Although females have been consistently larger than males in both populations, size distribution patterns differed in the two populations. Variations in the size of turtles between conspecific populations can reflect adaptations to environments, indicate variation in biotic (e.g., food availability and stream quality) and/or abiotic factors (e.g., water temperature, seasonality and hydrodynamics) associated with habitat (LINDEMAN, 1996; ROWE, 1997; TUCKER et al., 1998; Aresco & Dobie, 2000; Lubcke & Wilson, 2007). In a population of Mesoclemmys vanderhaegei studied in ponds near a silvicultural system in southeastern Brazil, average CL was 30% longer in females and 20% longer in males, in comparison to the values obtained in the present study (MARQUES et al., 2013). The streams evaluated in the two sampled areas are visually similar, but biotic and abiotic aspects of these water bodies that we did not measure may be responsible for the observed differences. LUBCKE & WILSON (2007) observed that food availability is higher in environments with muddy bottom substrates, which may be the reason for the size differences of three conspecific populations of Actinemys marmorata (Baird & Girard, 1852) in northern California, as well as higher temperatures in some streams. Visually, the streams sampled in the EESA have muddy bottom substrates and therefore appear to be more productive, while those in PNCG are sandy, which may explain the differences observed in the size distribution of the two populations.

Upon jointly analyzing body mass and eight morphometric variables frequently used in studies of chelonians (CL, HW, MCW, MPL, MPW, MHS, PCL, and TL; Tab. I), we found that males and females of Mesoclemmys vanderhaegei can be distinguished from each other without using more variables, even though the size distribution pattern differs in the two populations under study. However, when more variables were added to the models, only two of the eight above mentioned variables - MPL and PCL - were selected by the best model. In addition to carapace and tail length, represented by CMP and PCL, respectively, our best model predicted that other morphometric variables related to the head (TSL and TYL), plastron (MPL and PLW), and bridge (MBL and MVSL) can also be used to evidence differences between male and female individuals of M. vanderhaegei. Other variables considered important to distinguish between males and females (e.g., CPD and MHS) were not selected by the best model. However, these variables were present in models with $\Delta AIC < 2$, indicating that they are also important for distinguishing the sexes in this species. For the emydid Trachemys dorbigni (Duméril & Bibron, 1835) CPD was considered an important variable of secondary sexual dimorphism to distinguish between the sexes, because it involves reproductive aspects (BAGER et al., 2010).

Reproductive aspects are among the factors that offer a more compelling explanation for different use of the environment, and hence, for sexual dimorphism. Females travel in search of nesting areas, while males do so in search of females for mating (GIBBONS, 1990; WARISS *et al.*, 2012). The morphological particularities of males are related to territorial or sexual disputes, courtship, and mating. In females, these activities deplete nutrient reserves that are needed for reproduction, for example, to produce larger or more numerous eggs, as proposed by the theory of reproductive effort (RALLS, 1976; SCHOENER et al., 1982) or the theory of reproductive advantage (BERRY & SHINE 1980; GIBBONS et al., 1982; CONGDON & GIBBONS, 1983; GIBBONS & GREENE, 1990; GIBBONS & LOVICH, 1990; BONNET et al., 2001; LAGARDE et al., 2003; STEVENSON et al., 2007). Thus, selection for increased productivity may produce larger females (BERRY & SHINE, 1980; GIBBONS & LOVICH, 1990). In addition, females with larger shells are more protected from predators (BARROS et al., 2012). These aspects would help to explain the relatively longer and higher shell of the females of Mesoclemmys vanderhaegei (here represented by the variables CCW, CL, MHS, MPL, and MPW).

The CL – a usual indicator of size in chelonians – was previously used for standardization of all other variables and therefore could not be used in the multi-models. However, the MPL is also a size indicator in these organisms and was selected by the best model. Similarly, it was observed in the aquatic geoemydid *Malayemys macrocephala* (Gray, 1859), from Asia, that the CL was important to distinguish the sexes, along with morphometric variables related to the plastron, such as the anal scute length (ANSL), maximum plastral lobe length (PLL), and femoral (FemL) and pectoral scute lengths (Pecl) (BROPHY, 2006).

Our best model and the other 46 models with Δ AIC<2 selected 29 out of 34 morphometric variables, indicating that the morphometric difference between males and females of *Mesoclemmys vanderhaegei* is so conspicuous that it is reflected by almost all the variables considered here. However, for the sake of practicality males in this species can be distinguished from females using a set of only seven variables, two of them frequently used in studies of chelonians, and five others not commonly used. On the other hand, we have shown that variables related to the carapace frequently used to describe the size of chelonians – such as MCW and MHS – did not prove to be useful for differing between the sexes in *M. vanderhaegei*. Overall, our results contribute to the improvement of the morphometric protocols for this species.

Acknowledgments. The authors thank the staff of the Instituto Chico Mendes para Conservação da Biodiversidade (ICMBio) at Parque Nacional da Chapada do Guimarães and Estação Ecológica Serra das Araras for their support in the collection of field data. We also thank to the National Centre for Research and Conservation of Reptiles and Amphibians (RAN) for the collecting permit (SISBIO #25225-2); to the Animal Research Ethics Committee of the Universidade Federal do Mato Grosso for the authorization nº 23108026254/08-0; to the Fundação de Amparo à Pesquisa do Estado de Mato Grosso-FAPEMAT, through the "Edital de Apoio a Programa de Pós Graduação stricto sensu CAPES/FAPEMAT Nº 009/2014", for the financial support to professional translation. ESB thanks the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for a doctoral scholarship at the time of data acquisition, and thanks the Programa Nacional de Pós-Doutorado (PNPD) for a post-doctoral scholarship. CS thanks Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for a Research Productivity Grant, Level 2 (process #309541/2012-3).

REFERENCES

- ANDERSON, M. J. 2001. A new method for non-parametric multivariate analysis of variance in ecology. Austral Ecology 26(1):32-46.
- ARESCO, M. J. & DOBIE, J. L. 2000. Variation in shell arching and sexual size dimorphism of river cooters, *Pseudemys concinna*, from two river systems in Alabama. Journal of Herpetology 34(2):313-317.
- BAGER, A.; FREITAS, T. R. O. & KRAUSE, L. 2010. Morphological characterization of adults of Orbigny's slider *Trachemys dorbignyi* (Duméril & Bibron 1835) (Testudines Emydidae) in southern Brazil. Tropical Zoology 23(2):1-14.
- BAGER, A.; LUCAS, P. S.; COSTA, A.; LIMA, J. C. & SILVEIRA, L. S. 2016. Geographical variation in the morphology and sexual dimorphism of *Acanthochelys spixii* (Testudines, Chelidae) in Brazil. Tropical Zoology 29(2):76-86.
- BARROS, M. S.; RESENDE, L. C.; SILVA, A. G. & FERREIRA JUNIOR, P. D. 2012. Morphological variations and sexual dimorphism in *Chelonoidis carbonaria* (Spix, 1824) and *Chelonoidis denticulata* (Linnaeus, 1766) (Testudinidae). Brazilian Journal of Biology 72(1):153-161.
- BERRY, J. F. & SHINE, R. 1980. Sexual dimorphism and sexual selection in turtles (Order Testudines). Oecologia 44(2):185-191.
- BONNET, X.; LAGARDE, F.; HENEN, B. T.; CORBIN, J.; NAGY, K. A.; NAULLEAU, G.; BALHOUL, K.; CHASTEL, O.; LEGRAND, A. & CAMBAG, R. 2001. Sexual dimorphism in steppe tortoises: influence of the environment and sexual selection on body shape and mobility. Biological Journal of the Linnean Society 72(8):357-372.
- BOUR, R. & ZAHER, H. 2005. A new species of *Mesoclemmys*, from the open formations of Northeastern Brazil (Chelonii, Chelidae). Papéis Avulsos de Zoologia 45(24):295-311.
- BRITO, E. S.; SOUZA, F. L. & STRÜSSMANN, C. 2016. Feeding Habits of *Mesoclemmys vanderhaegei* (Testudines: Chelidae). Acta Herpetologica 11(1):1-13.
- BRITO, E. S.; STRÜSSMANN, C. & PENHA, J. M. F. 2009. Population structure of *Mesoclemmys vanderhaegei* (Bour, 1973) (Testudines: Chelidae) in the Cerrado of Chapada dos Guimarães, Mato Grosso, Brazil. Biota Neotropica 9(4):245-248.
- BRITO, E. S.; VOGT, R. C.; VALADÃO, R. M.; FRANÇA, L. F.; PENHA, J. & STRÜSSMANN, C. 2018. Population Ecology of the Freshwater Turtle *Mesoclemmys vanderhaegei* (Testudines: Chelidae). Herpetological Conservation and Biology 13(2):355-365.
- BROPHY, T. R. 2006. Allometry and sexual dimorphism in the Snaileating turtle *Malayemys macrocephala* from the Chao Phraya River Basin of Central Thailand. Chelonian Conservation and Biology 5(1):159-165.
- BURNHAM, K. P. & ANDERSON, D. R. 2002. Model selection and multimodel inference: A practical information-theoretic approach. New York, Springer-Verlag, 488 p.
- CAGLE, F. R. 1939. A system of marking turtles for future identification. Copeia 1939(3):170-173.
- CALCAGNO, V. & MAZANCOURT, C. 2010. glmulti: An R Package for Easy Automated Model Selection with (Generalized) Linear Models. Journal of Statistical Software 34(12):1-29.
- CONGDON, J. D. & GIBBONS, J. W. 1983. Relationships of reproductive characteristics to body size in *Pseudemys scripta*. Herpetologica 39:147-151.
- DUSTMAN, E. 2013. Sex identification in the Common Snapping turtle (*Chelydra serpentina*): a new technique and evaluation of previous methods. Herpetological Review 44:235-238.
- ERNST, C. H. 1971. Sexual cycles and maturity of the turtle, *Chrysemys picta*. The Biological Bulletin 140(2):191-200.
- FITCH, H. S. 1981. Sexual size differences in reptiles. Miscellaneous Publications of the Museum of Natural History University of Kansas 70(59):1-72.
- FONSECA, C. P. 2005. Caracterização dos ecossistemas aquáticos do Cerrado. *In*: SOUZA-SILVA, J. C. & FELFILI, J. M. eds. Cerrado: Ecologia, Biodiversidade e Conservação. Brasília, Ministério do Meio Ambiente, p. 416-429.
- FORSMAN, A. & SHINE, R. 1995. Sexual size dimorphism in relation to frequency of reproduction in turtles (Testudines: Emydidae). Copeia 1995(3):727-729.
- GARBIN, R. G.; KARLGUTH, D. T.; FERNANDES, D. S. & PINTO, R. R. 2016. Morphological variation in the Brazilian Radiated Swamp Turtle

Acanthochelys radiolata (Mikan, 1820) (Testudines: Chelidae). Zootaxa 4105(1):045-064.

- GIBBONS, J. W. 1990. Sex ratio and their significance among turtle populations. *In*: GIBBONS, J. W. ed. Life history and ecology of the Slider turtle. Washington, Smithsonian Institution Press, p. 171-182.
- GIBBONS, J. W. & GREENE, J. L.1990. Reproduction in the slider and other species of turtles. *In*: GIBBONS, J. W. eds. Life history and ecology of the Slider Turtle. Washington, Smithsonian Institution Press, p. 124-134.
- GIBBONS, J. W. & LOVICH, J. E. 1990. Sexual dimorphism in turtles with emphasis on the Slider Turtle (*Trachemys scripta*). Herpetological Monographs 4:1-29.
- GIBBONS, J. W.; GREENE, J. L. & PATTERSON, K. R. 1982. Variation in reproductive characteristics of aquatic turtles. Copeia 1982:776-784.
- IVERSON, J. B. 1984. Proportional skeletal mass in turtles. Florida Scientist 47:1-11.
- JACKSON, D. A. 1993. Stopping rules in principal components analysis: A comparison of heuristical and statistical approaches. Ecology 74(8):2204-2214.
- LAGARDE, F.; BONNET, X.; HENEN, B.; LEGRAND, A.; CORBIN, J.; NAGY, K. & NAULLEAU, G. 2003. Sex divergence in space utilization in the steppe tortoise (*Testudo horsfieldi*). Canadian Journal of Zoology 81(3):380-387.
- LINDEMAN, P. V. 1996. Comparative life history of Painted Turtles (*Chrysemys picta*) in two habitats in the inland Pacific Northwest. **Copeia 1996**:114-130.
- LOVICH, J. L.; ERNST, C. H.; ZAPPALORTI, R. T. & HERMAN, D. W. 1998. Geographic variation in growth and sexual size dimorphism of Bog turtles (*Clemmys muhlenbergii*). American Midland Naturalist 139(1):69-78.
- LUBCKE, G. M. & WILSON, D. S. 2007. Variation in shell morphology of the Western pond turtle (*Actinemys marmorata* Baird and Girard) from three aquatic habitats in Northern California. Journal of Herpetology 41(1):107-114.
- McCord, W. P.; JOSEPH-OUNI, M. & LAMAR, W. W. 2001. Taxonomic reevaluation of *Phrynops* (Testudines: Chelidae) with the description of two new genera and a new species of *Batrachemys*. **Revista de Biologia Tropical 49**(2):715-764.
- MARQUES, T. S.; BÖHM, S.; BRITO, E. S.; CABRERA, M. R. & VERDADE, L. M. 2014. Mesoclemmys vanderhaegei (Bour 1973) – Vanderhaege's Toadheaded Turtle, Karumbé-hy. In: RHODIN, A. G. J.; PRITCHARD, P. C. H.; VAN DIJK, P. P.; SAUMURE, R. A.; BUHLMANN, K. A.; IVERSON, J. B. & MITTERMEIER, R. A. eds. Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 5:083.1-8.
- MARQUES, T. S.; LARA, N. R. F.; BASSETTI, L. A. B.; FERRONATO, B. O.; MALVÁSIO, A. & VERDADE, L. M. 2013. Population structure of *Mesoclemmys vanderhaegei* (Testudines, Chelidae) in a silvicultural system in southeastern Brazil. Herpetology Notes 6:179-182.
- McKNIGHT, D. T.; HOWELL, H. J.; HOLLENDER, E. C. & LIGON, D. B. 2017. Good vibrations: a novel method for sexing turtles. Acta Herpetologica 12(1):117-121.
- MOLINA, F. B. 1998. Comportamento e biologia reprodutiva dos cágados Phrynops geoffroanus, Acanthochelys radiolata e Acanthochelys spixii (Testudines, Chelidae) em cativeiro. Revista de Etologia 1998:25-40.
- MOLINA, F. B.; MACHADO, F. A. & ZAHER, H. 2012. Taxonomic validity of Mesoclemmys heliostemma (McCord, Joseph-Ouni & Lamar, 2001)

(Testudines, Chelidae) inferred from morphological analysis. **Zootaxa 3575**(1):63-77.

- OKSANEN, J.; BLANCHET, F. G.; KINDT, R.; LEGENDRE, P.; MINCHIN, P. R.; O'HARA, R. B.; SIMPSON, G. L.; SOLYMOS, P.; STEVENS, M. H. H. & WAGNER H. 2012. Vegan: Community Ecology Package. R package version 2.0-2. Available at http://CRAN.Rproject.org/package0vegan>.
- R DEVELOPMENT CORE TEAM. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at http://www.R-project.org/Accessed on 01 June 2016.
- RALLS, K. 1976. Mammals in which females are larger than males. Quarterly Review of Biology 51(2):245-276.
- READEL, A. M.; DRESLIK, M. J.; WARNER, J. K.; BANNING, W. J. & PHILLIPS, C. A. 2008. A quantitative method for sex identification in Emydid turtles using secondary sexual characters. Copeia 3:643-647.
- RHODIN, A. G. J.; MITTERMEIER, R. A. & MCMORRIS, J. R. 1984. *Platemys macrocephala*, a new species of chelid turtle from Central Bolivia and the Pantanal region of Brazil. Herpetologica 40:38-46.
- RIBEIRO, J. F. & WALTER, B. M. T. 2001. As matas de galeria no contexto do bioma Cerrado. In: RIBEIRO, J. F.; FONSECA, C. E. L. & SILVA, J. C. S. eds. Cerrado: caracterização e recuperação de matas de galeria. Planaltina, Embrapa Cerrados, p. 29-47.
- RODRIGUES, J. F. M.; SOARES, D. O. & SILVA, J. R. F. 2014. Sexing freshwater turtles: penile eversion in *Phrynops tuberosus* (Testudines: Chelidae). Acta Herpetologica 9(2):259-263.
- ROWE, J. W. 1997. Growth rate, body size, sexual dimorphism and morphometric variation in four populations of Painted Turtles (*Chrysemys pictabelli*) from Nebraska. American Midland Naturalist 138:174-188.
- SCHOENER, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. Science 155(3761):474-477.
- SCHOENER, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. **Ecology 49**(4):704-726.
- SCHOENER, T. W. 1977. Competition and the niche. *In*: GANS, C. & TINKLE, D. W. eds. Biology of the Reptilia. New York, Academic Press, p. 35-136.
- SCHOENER, T. W.; SLADE, J. B. & STINSON, C. H. 1982. Diet and sexual dimorphism in the very catholic lizard genus, *Leiocephalus* of the Bahamas. Oecologia 53(2):160-169.
- SHINE, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. The Quarterly Review of Biology 64(4):419-431.
- STEVENSON, P. R.; BORDA, C. A.; ROJAS, A. M. & ALVAREZ, M. 2007. Population size, habitat choice, and sexual dimorphism of the Amazonian tortoise (*Geochelone denticulata*) in Tinigua Park, Colombia. Amphibia-Reptilia 28(2):217-226.
- TUCKER, J. K.; JANZEN, F. J. & PAUKSTIS, G. L. 1998. Variation in carapace morphology and reproduction in the Red-Eared Slider *Trachemys scripta elegans*. Journal of Herpetology 32(2):294-298.
- VINKE, T.; VINKE, S. & KOHLER, G. 2013. What is known about *Mesoclemmys vanderhaegei* (Bour, 1973): a systematic review of the available literature. Paraquaria Natural 1(2):21-31.
- WARISS, M.; ISAAC, V. J. & PEZZUTI, J. C. B. 2012. Habitat use, size structure and sex ratio of the spotlegged turtle, *Rhinoclemmys punctularia punctularia* (Testudines: Geoemydidae), in Algodoal Maiandeua Island, Pará, Brazil. **Revista de Biologia Tropical 60**(1):413-424.