



Short communication

How giant are giant armadillos? The morphometry of giant armadillos (*Priodontes maximus* Kerr, 1792) in the Pantanal of BrazilArnaud Leonard Jean Desbiez^{a,b,c,*}, Gabriel Favero Massocato^{a,c,d}, Danilo Kluyber^{a,c,e}, Camila Do Nascimento Luba^{a,f}, Nina Attias^{a,g}^a Instituto de Conservação de Animais Silvestres (ICAS), Rua Licuala 622, 79046150, Campo Grande, Mato Grosso do Sul, Brazil^b Royal Zoological Society of Scotland (RZSS), Murrayfield, Edinburgh, EH12 6TS, United Kingdom^c Instituto de Pesquisas Ecológicas (IPÊ), Rodovia Dom Pedro I, km 47, 12960-000, Nazaré Paulista, São Paulo, Brazil^d Houston Zoo, 6200 Hermann Park Drive, Houston, TX, 77030, USA^e Naples Zoo at Caribbean Gardens, 1590 Goodlette-Frank Rd, Naples, FL, 34102, USA^f Programa de Pós-Graduação em Medicina Veterinária – Clínica e Reprodução Animal, Universidade Federal Fluminense, Avenida Almirante Ary Parreiras, 507, 24220-000, Niterói, Rio de Janeiro, Brazil^g Programa de Pós-Graduação em Biologia Animal, Universidade Federal do Mato Grosso do Sul, Cidade Universitária, Av. Costa e Silva, Campo Grande, Mato Grosso do Sul, Brazil

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ABSTRACT

Morphometrics is the quantitative study of organisms shape and size. Intrinsic (e.g. age and sex) and extrinsic (e.g. abiotic conditions) factors can be related to morphological diversity and can aid in the study of species biology and ecology. Giant armadillos have rarely been captured in the wild and very little is known about the species. Here we aimed to characterize body measurements of free-living giant armadillos (*Priodontes maximus*) in mid-western Brazil and evaluate how these measurements vary between sexes and age classes to gain insights on the species biology and ecology. We captured 28 armadillos in the study area, 18 adults (9 males, 9 females) and 10 subadults (6 males, 4 females) and assessed twenty-five different morphometric measurements for each captured armadillo. To evaluate if age class and sex of adult individuals can be differentiated by a concise set of morphometric measurements we used Linear Discriminant Analyses. We encountered significant morphometric differentiation between age classes and report seven parameters that best discriminate individuals between age classes which may allow the identification of individual's age class in future studies. The wide morphometric variation in subadults could indicate that individuals have a long developmental process between weaning and sexual maturity. Morphometric differentiation between sexes was possible through the association of three morphological parameters and adult males are larger and heavier than females. Although we were limited by the number of animals sampled in previous studies, females presented similar body mass across studied sites, while males presented variation of up to ten kilos across the species distribution. This indicates that the degree of sexual dimorphism can vary among localities and raises interesting ecological questions regarding the species reproductive system. This variation can be related to abiotic factors (e.g. latitude, temperature and topography), differences in productivity among biomes (i.e. resource abundance and distribution), population density, and/or genetic variation between populations and should be explored further. We propose the measurements used here be used as standard measurements for this species since it encompasses all of the most distinctive features of the species and allows a full morphological characterization, enabling the future comparison between populations of this widely distributed species.

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Morphometrics is the quantitative description and interpretation of organisms shape and size (Rohlf, 1990). It allows us to understand how shape and size relate with each other and with other intrinsic factors such as age and sex of individuals aiding, for example, in species developmental studies (Moraes, 2003; Rohlf, 1990). These types of measurements are also necessary for the

description of species and can aid in the study of species taxonomy and phylogenetics (e.g. Geise et al., 2005). Since biotic and abiotic factors can influence animal morphometry, specimens from different areas may differ from one another in size and morphology. Temperature, for example, is known to have a relationship with body size in taxonomic groups with broad geographical ranges (e.g. Pagh et al., 2018; Rodríguez et al., 2008; Storz et al., 2001). Populations at high latitudes, at lower ambient temperatures, tend to have individuals with comparatively larger body sizes (Bergmann's rule). Hence, morphometrics can be a useful tool to study variations among populations of species with wide ranging geographical distributions (Franicevic et al., 2005; Storz et al., 2001).

Species of the super-order Xenarthra are terrestrial mammals with unique morphological attributes that are mainly related to its specialized diet and digging activities (Milne et al., 2009; Möller-Krull et al., 2007). This group is composed by the orders Cingulata (armadillos) and Pilosa (anteaters and sloths). Armadillos are easily distinguishable from other groups by the presence of a carapace, formed by ossified dermal tissue, and fossorial habits, excavating the soil to forage and to build burrows where they can rest and shelter from unfavorable conditions (Eisenberg and Redford, 1999). Giant armadillos (*Priontodes maximus* Kerr, 1792) are found over much of South America – in 11 different countries – in habitats ranging from tropical forest to open savanna (Abba and Superina, 2010). In Brazil, this species can be found in the Amazon, Atlantic Forest, Cerrado and Pantanal ecoregions (Fonseca et al., 1996). Nevertheless, despite its wide geographical distribution, giant armadillos are always rare even in habitats considered pristine (Meritt, 2006). The species is currently classified as “Vulnerable” (A2cd) by the IUCN Red List of Threatened Species (Anacleto et al., 2014). The giant armadillo can reach up to 150 cm in total length (75–100 cm body length, 50 cm tail) and have a body mass usually between 28 and 50 kg, but may reach up to 60 kg (Carter et al., 2016; Emmons and Feer, 1997; Nowak, 1999). This species is by far the largest species of extant armadillos (Emmons and Feer, 1997). One of the most striking features of the species, besides its size, are the large scimitar-shaped fore-claws, the third of which is greatly enlarged and can be as long as 20.3 cm (Carter et al., 2016). The carapace of giant armadillos has 11 to 13 movable bands, dark-brown color with a light-colored stripe near its border (Nowak, 1999). The scale pattern between dark and light parts of the carapace is an individual identification method commonly used for this species (Noss et al., 2004).

The morphometry of giant armadillos has been characterized mainly through isolated captures of individuals, without any standardization. Due to their low densities, nocturnal and fossorial habits, giant armadillos are rarely seen (Eisenberg and Redford, 1999; Noss et al., 2004; Silveira et al., 2009) and their large burrows are often the only evidence of their presence and have been the focus of several studies (Anacleto, 1997; Carter, 1983; Carter and Encarnação, 1983; Desbiez and Kluyber, 2013; Massocato and Desbiez, 2017). Overall, researchers have rarely attempted to capture giant armadillos, and only a small number of individuals have been captured in previous studies (e.g. Anacleto, 1997; Carter and Encarnação, 1983; Encarnação, 1986; Leite-Pitman et al., 2004; Silveira et al., 2009). From these captured individuals, there is little information on body measurements. One exception is the work done at Emas National Park (Goiás state - Brazil; Fig. 1), where seven giant armadillos were captured and measured. At this site, giant armadillos presented sexual dimorphism in body weight and size, with males (155.90 cm, 44.40 kg) larger and heavier than females (137.74 cm, 28 kg; Silveira et al., 2009).

Given the lack of information and standardization on the morphometrics of *P. maximus*, here we aim to characterize the morphometry of free-living individuals of this species in mid-western Brazil and evaluate how these measurements vary within the pop-

ulation, e.g. between sexes and age classes. Furthermore, we aim to compare the body mass estimates of the individuals at our study area with those of previous studies at other localities, allowing the description of the morphometric variation of the species along part of its broad geographical distribution. Animal body size is shaped by multiple selective pressures, which may have functional consequences in an array of life history traits (Clutton-Brock and Harvey, 1983). As seen in other animals with broad distribution ranges, body size can be influenced by different factors (e.g. Storz et al., 2001; Yom-Tov and Nix, 1986), we therefore expect giant armadillo body mass to differ among ecoregions due to varying abiotic conditions (Rodríguez et al., 2008).

This study was carried out between July 2010 and January 2018, in a 300-km² area that includes ten traditionally managed cattle ranches (19° 16' 60" S, 55° 42' 60" W) in the Nhecolândia sub-region of the Brazilian Pantanal (Fig. 1). The Pantanal is a complex of ecosystems, located in Midwestern Brazil, composed by a highly heterogeneous landscape that is influenced by neighboring biomes. Like in other parts of the Pantanal, a mosaic of different habitats that includes open grassland, scrub grassland, scrub forest, and semi-deciduous forest composes the landscape of the study area (Abdon et al., 1998). Mean temperature is 25.4° C, climate is classified as semi-humid tropical (Aw), with a hot, rainy season (October to March), and warm drier season (April to September; Soriano, 2000). The area lacks watercourses, but there is widespread flooding during the rainy season.

We performed active searches by foot or pickup trucks looking for signs (tracks, feces and burrows) of giant armadillos. Armadillos were captured using funnel traps that were placed at the entrance of burrows with evidence of recent activity (following Carter, 1985; Silveira et al., 2009). Once captured, animals were temporarily placed in ventilated wooden boxes (Superina et al., 2014) reinforced with metal sheeting and then anaesthetized through an intramuscular injection in the hind limbs. The anesthetic protocol was composed of Butorphanol 10 mg/ml (0.1 mg/kg), Detomidine 10 mg/ml (0.1 mg/kg) and Midazolam 5 mg/ml (0.2 mg/kg; D. Kluyber pers. comm.). While immobilized, we collected information on age, sex, body mass and morphometric measurements (Table 1). To ensure standardization, the same team member [AD] performed the measurements of all individuals using a graduated flexible measuring tape and a 100 kg digital scale. For individuals captured more than once, we used only the set of measurements obtained in its first capture event, or the set of measurements taken by the designated team member [AD].

We captured 28 giant armadillos in the study area, 18 adults (9 males, 9 females) and 10 subadults (6 males, 4 females). Subadults were classified as prepubescent individuals that were no longer under its mothers care. We assessed twenty-five morphometric measurements for each captured armadillo, by incorporating additional measurements to those used in the work of Silveira et al. (2009). Morphometric measurements are described in detail (Table A.1; and partially illustrated – Fig. A.1) in the Supplementary Material A. To characterize giant armadillo's morphological variation, we estimated the mean (\pm standard deviation), the range and the standard error for each measurement for each age class and sex (Table 1).

We log-transformed the raw measurements prior to the analyses to normalize the distribution and to equalize variances in the dataset (Gotelli and Ellison, 2004). To evaluate the correlation structure between morphometric measurements we used a correlation matrix and excluded variables with correlation > 0.7. After this initial selection, we used Linear Discriminant Analyses to evaluate if age class and sex of adult individuals can be differentiated by a concise set of morphometric measurements. We selected the smallest set of variables that increased the percentage of correct jackknifed classification of groups and presented the highest

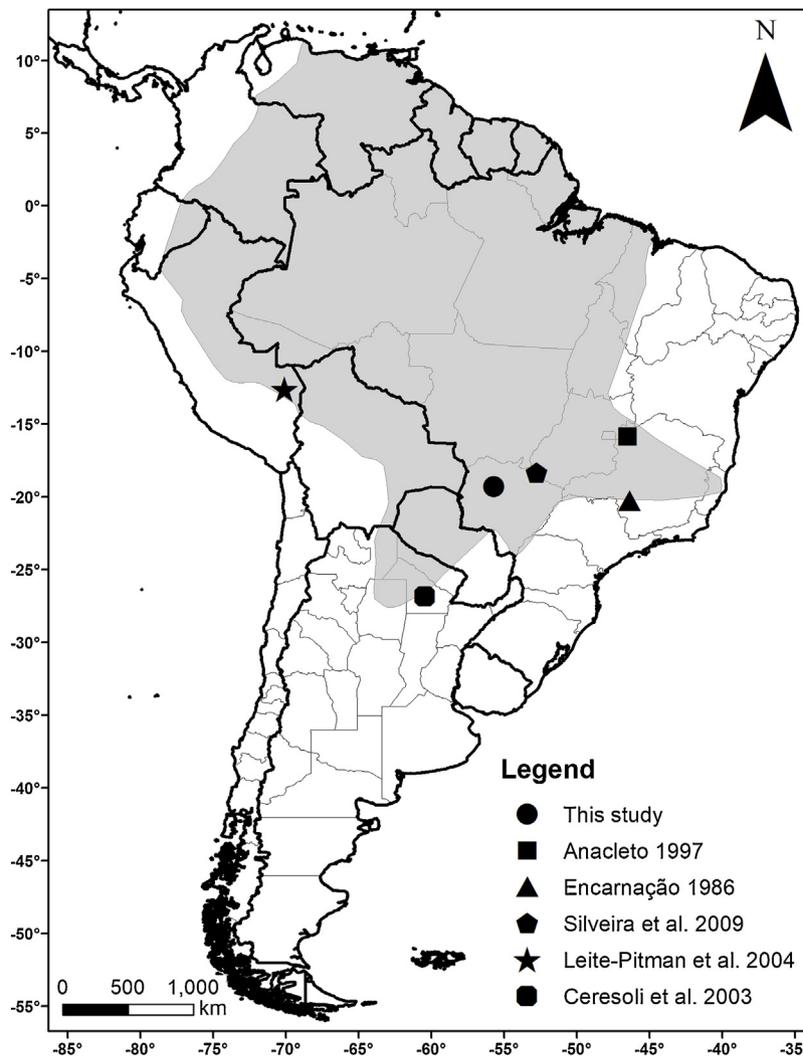


Fig. 1. Giant armadillo (*Priodontes maximus*) distribution in South America (gray area), location of our study site (circle) and locations of previous studies that also provide giant armadillo morphometric measurements.

eigenvalue among models. We plotted the scores of the selected discriminant function to provide a measure of the relative discriminatory power of the selected parameters. Statistical analyses were performed using Systat 11 and graphs were plotted in R. Finally, to characterize morphometric variation throughout the species range, we present all available body measurements presented in previous studies in Supplementary Material B (Table B.1). Nevertheless, due to the scarcity of data and the lack of measurements standardization, we restricted our discussion to the variation of mean body mass between studies (Fig. 1). Maps were created using ArcGis 10.5.

In the present study, we provide a thorough characterization of the morphometry of *P. maximus*, characterizing adult and subadult individuals of both sexes (Table 1). We classify subadults as pre-pubescent individuals that did not present signs of sexual activity. Subadult females presented smaller vulvar diameter and poorly developed teats, when compared to sexually active adults. Subadult males presented azoospermatic ejaculation and relatively shorter penis length (13.62 ± 3.38 cm), when compared to sexually active adults. The subadult classification encompasses all prepubescent individuals that are no longer under its mothers care, hence, this class presents a wide body mass range (18–30.4 kg). Therefore, small adults and large subadults can present similar body mass (Sup. Mat. C; Fig. C.1). The association between the above mentioned morphological characteristics and information on sexual

activity can be helpful for age class determination. Furthermore, the discriminant analysis revealed significant morphometric differentiation between age classes (Wilk's $\lambda = 0.05$, Approx. $F = 29.74$, $df = 7$, $p < 0.01$; Fig. 2). This analysis indicated body mass (BM), head circumference (HC), carapace length (CL), total body length - ventral (TBLV), thorax circumference (TC), total body length - dorsal (TBLD) and length of the front claw #3 (C#3) as the seven parameters that best discriminate individuals between age classes. The following standardized discriminant equation (D) provided a Jackknifed classification matrix with 100% of correct classification of individuals to the corresponding age classes: $D = -2.177 \cdot \text{TBLD} - 2.071 \cdot \text{TBLV} + 1.911 \cdot \text{BM} + 1.873 \cdot \text{HC} + 1.365 \cdot \text{TC} + 1.11 \cdot \text{CL} + 0.986 \cdot \text{C\#3}$. Values of factor loadings of each parameter are proportional to its contribution to the discriminant function. Hence, the parameters with the highest relative contributions to the observed pattern of multivariate differentiation between age classes are TBLD and TBLV. The wide morphological variability in subadults (Fig. 2) could indicate that individuals have a long developmental process between weaning and sexual maturity.

Morphometric differences between sexes were also evidenced by discriminant analysis (Wilk's $\lambda = 0.17$, Approx. $F = 13.22$, $df = 3$, $p < 0.01$; Fig. 2). Carapace length (CL), thorax circumference (TC) and hindlimb length (HL) were the parameters that best discriminated individuals between sexes according to the following standardized

Table 1
Body measurements of giant armadillos (*Priodontes maximus*) captured at Baía das Pedras ranch, Aquidauana, Brazil, between October 2011 and January 2018. We present the measurement's mean \pm SD, its range and standard error. Measurements are given in centimeters and body mass in kilograms.

Body Measurement	Adult (N = 18)				Subadult (N = 10)			
	Mean	Std. error	Mean female	Mean male	Mean	Std. error	Mean female	Mean male
Body mass	33.18 \pm 2.51 (28.6 – 36.6)	0.59	31.68 \pm 1.78	34.69 \pm 2.27	24.57 \pm 4.15 (18 – 30.4)	1.31	24.2 \pm 4.23	24.82 \pm 4.49
Body length - ventral	81.53 \pm 4.23 (72 – 90)	0.99	79.5 \pm 3.7	83.56 \pm 3.9	76.12 \pm 6.08 (68 – 86)	1.92	70.67 \pm 2.51	79.4 \pm 5.08
Total body length - ventral	135.91 \pm 5.44 (123 – 146)	1.28	133 \pm 4.71	139.19 \pm 4.36	127.22 \pm 6.31 (119 – 135)	1.99	122.67 \pm 3.05	129.5 \pm 6.42
Body length - dorsal	92.19 \pm 8.17 (70 – 99)	1.92	88.12 \pm 10.1	96.25 \pm 1.98	84.33 \pm 9.77 (63 – 93)	3.09	88.5 \pm 5.45	81 \pm 11.73
Total body length - dorsal	146.11 \pm 8.22 (118 – 153)	1.93	145.78 \pm 4.79	146.44 \pm 10.97	139.28 \pm 7.36 (127 – 149)	2.33	141 \pm 9.76	137.9 \pm 5.62
Tail length	53.31 \pm 2.94 (49 – 60)	0.69	52.87 \pm 3.72	53.75 \pm 2.05	50.58 \pm 2.67 (47 – 56)	0.85	51.87 \pm 3.70	49.72 \pm 1.56
Carapace length	76.39 \pm 6.94 (70 – 98)	1.64	72.58 \pm 1.36	79.25 \pm 8.15	61.31 \pm 15 (25 – 72)	4.74	67 \pm 5	57.9 \pm 18.51
Carapace width	58.88 \pm 4.34 (50 – 64)	1.02	56.08 \pm 4.59	61.28 \pm 2.36	47.62 \pm 7.93 (32 – 58)	2.51	52.33 \pm 6.66	44.8 \pm 7.82
Thorax circumference	81.61 \pm 7.93 (72 – 98)	1.87	78.86 \pm 6.94	84.36 \pm 8.39	73.33 \pm 5.19 (67 – 84)	1.64	70.67 \pm 3.21	74.67 \pm 5.71
Abdomen circumference	85.97 \pm 6.36 (76 – 96)	1.50	85.78 \pm 7.19	86.12 \pm 6.06	78.61 \pm 6.66 (71 – 90)	2.11	77.67 \pm 3.78	79.08 \pm 8.03
Head circumference	29.97 \pm 2.67 (23 – 36)	0.63	30 \pm 0.96	29.94 \pm 3.67	28.1 \pm 1.45 (26 – 30)	0.46	27.62 \pm 1.79	28.41 \pm 1.24
Head length	20.44 \pm 0.95 (18 – 22)	0.22	20.28 \pm 1.09	20.62 \pm 0.79	20.3 \pm 0.82 (19 – 22)	0.26	20.25 \pm 0.5	20.33 \pm 1.03
Distance between eyes	11.36 \pm 1.03 (9 – 12.5)	0.24	11.25 \pm 0.76	11.44 \pm 1.24	10.69 \pm 0.84 (9 – 11.5)	0.27	10.5 \pm 0.5	10.8 \pm 1.04
Ear length	5.37 \pm 0.87 (4 – 7)	0.20	5.25 \pm 0.6	5.5 \pm 1.1	5.5 \pm 1.03 (4.5 – 7)	0.32	5.12 \pm 1.25	5.75 \pm 0.88
Ear width	4.37 \pm 0.69 (3.5 – 6)	0.16	4.06 \pm 0.32	4.69 \pm 0.84	4.37 \pm 0.49 (3.7 – 5)	0.16	4.62 \pm 0.47	4.2 \pm 0.47
Neck circumference	34.9 \pm 1.40 (33 – 38)	0.33	34.6 \pm 1.34	35.25 \pm 1.48	32.23 \pm 1.37 (31 – 34)	0.43	32.5 \pm 1.29	32.05 \pm 1.51
Front limb length	24.53 \pm 4.11 (18.5 – 33)	0.97	24.62 \pm 3.92	24.44 \pm 4.56	22.67 \pm 2.55 (19 – 28)	0.81	22.25 \pm 1.26	23 \pm 3.39
Hinder limb length	31.12 \pm 2.25 (28 – 36)	0.53	30 \pm 2.14	32.25 \pm 1.83	29.4 \pm 3.66 (22 – 34)	1.16	30.25 \pm 3.3	28.83 \pm 4.07
Front claw #1	2.6 \pm 0.57 (1.5 – 3.5)	0.13	2.72 \pm 0.56	2.32 \pm 0.57	2.6 \pm 0.58 (1.3 – 3.5)	0.18	2.92 \pm 0.43	2.32 \pm 0.58
Front claw #2	4.26 \pm 0.79 (2.4 – 5.5)	0.19	4.32 \pm 0.88	4.12 \pm 0.63	4.2 \pm 0.29 (3.8 – 4.5)	0.09	4.25 \pm 0.29	4.16 \pm 0.32
Front claw #3	13.23 \pm 0.71 (12 – 14.5)	0.17	13.1 \pm 0.73	13.37 \pm 0.69	12.38 \pm 0.82 (11.5 – 14.3)	0.26	12 \pm 0.41	12.63 \pm 0.96
Front claw #4	4.95 \pm 0.80 (3 – 6)	0.14	5.22 \pm 0.56	4.32 \pm 0.99	5.07 \pm 0.43 (4.5 – 6)	0.14	5.12 \pm 0.25	5.04 \pm 0.58
Front claw #5	1.65 \pm 0.58 (1 – 3)	0.14	1.64 \pm 0.62	1.67 \pm 0.58	1.52 \pm 0.63 (1 – 2.7)	0.20	1.5 \pm 0.71	1.54 \pm 0.69
Penis / Clitoris length	–	–	6.68 \pm 1.45	36.06 \pm 7.02	–	–	4.5 \pm 0.87	13.62 \pm 3.38
Penis / Clitoris circumference	–	–	3 \pm 0	9.2 \pm 1.64	–	–	–	–

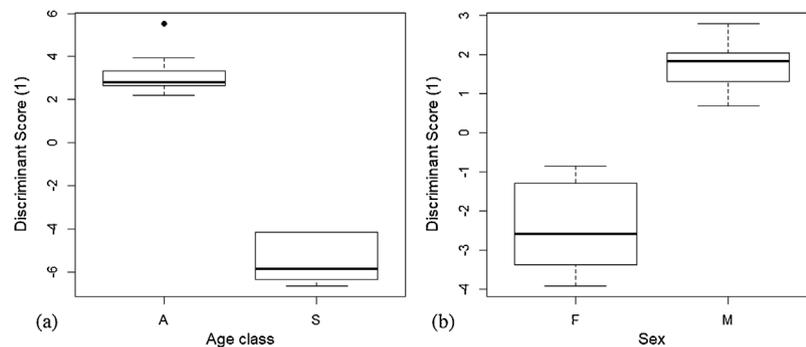


Fig. 2. Discrimination of (a) age class (A – adults, S – subadults, N = 28) and (b) adult sex (F – female, M – male, N = 18) of giant armadillos (*Priodontes maximus*) according to Linear Discriminant Functions. The parameters body mass, head circumference, carapace length, total body length - ventral, thorax circumference, total body length - dorsal and length of the front claw #3 are used for age class discrimination (a). The parameters carapace length, hindlimb length and thorax circumference are used for sex discrimination of adult individuals (b). Morphometric data collected at Baía das Pedras ranch, Aquidauana, Brazil, between October 2011 and January 2018.

discriminant equation (D): $D = 1.389*HL + 1.334*TC + 0.816*CL$. This equation provided a Jackknifed classification matrix with 100% of correct classification. This result corroborates the patterns encountered by [Silveira et al. \(2009\)](#), with adult males larger and heavier than females. These authors have reported sexual dimorphism in thorax circumference, which also proved to be an important parameter for sex differentiation in the present study. Hindlimb length was also evidenced as a discriminant parameter and is larger in adult males than in females, which could be related to the species reproductive behavior. In most species of armadillo, the male mounts on the top of the female for coitus (e.g. [Tomas et al., 2013](#)) hence, a greater hindlimb length could help males to mount over the rigid carapace of females in a more efficient manner. Sexual dimorphism has also been encountered for the insectivorous three-banded armadillo *Tolypeutes tricinctus* (with larger males; $N=20$; [Guimarães, 1997](#)) and, for the yellow armadillo *Euphractus sexcinctus* and the naked-tailed armadillo *Cabassou unicinctus* (with larger females in both species) in central Brazil ([Carter and Encarnaçao, 1983](#)). However, in the Pantanal, [Medri et al. \(2009\)](#) did not record differences between sexes for *E. sexcinctus* ($N=31$), nor did [Desbiez et al. \(2018\)](#) for *C. unicinctus* ($N=8$). In addition, sexual dimorphism was not detected for the screaming hairy armadillo *Chaetophractus vellerosus* ($N=136$) in Argentina ([Abba et al., 2011](#)) or for the nine-banded armadillo *Dasypus novemcinctus* in the United States ([McDonough and Loughry, 2001](#)). Similarly to other species of armadillo, besides the genitalia itself, there is no obvious morphological characteristics of *P. maximus* that allows the prompt differentiation between sexes, even though the species presents some degree of size-related sexual dimorphism ([Desbiez et al., 2018](#); [McDonough and Loughry, 2001](#); [Medri et al., 2011](#)). Male armadillos present one of the largest penises among mammals ([McDonough and Loughry, 2001](#)) and adult male giant armadillos presented average penis length of 36 ± 7.02 cm, 43% of its average ventral body length. It should be noted that adult female giant armadillos present a long clitoris (6.68 ± 1.45 cm) that could be mistaken for a penis by inexperienced researchers, particularly when reporting on camera traps.

At our study site, mean body mass for adult *P. maximus* was 34.69 ± 2.27 kg for males and 31.68 ± 1.78 kg for females ([Table 1](#); [Fig. C.1](#)). The mean body mass of adult females estimated in the present study is similar to those described in previous studies across Brazil, e.g. [Silveira et al. \(2009\)](#); 28 ± 2.71 kg) and [Encarnaçao \(1986\)](#); 32 kg; [Fig. 1](#); [Table B.1](#)). Nevertheless, the body mass of male individuals varied between this study and other ecoregions. Individuals in the Pantanal are smaller than those from the Cerrado. In the study of [Silveira et al. \(2009\)](#), at the Cerrado of Emas National Park ($18^{\circ} 19' S, 52^{\circ} 45' W$; [Fig. 1](#)), males (44.4 ± 4.1 kg) were nearly 10 kg heavier than the individuals captured at our study area. Armadillos recaptured at our study site in different seasons ($N=8$) presented weight variation of one to three kilograms ([Supplementary Material C](#); [Table C.1](#)). Hence, it is unlikely that the variation of up to 10 kg observed between study sites is related to differences in the time of capture of individuals and seasonal productivity. The single adult male captured by [Anacleto \(1997\)](#) at another Cerrado area located in the northwest of Minas Gerais state ($15^{\circ} 50' S, 46^{\circ} 30' W$) was also larger (41 kg) than the average adult male at our study site. In contrast, even though we have no information on its age class, the male captured in the Amazon, in southeastern Peru ($12^{\circ} 34' S 70^{\circ} 6' W$), by [Leite-Pitman et al. \(2004\)](#) had a body mass of 30 kg, similar to the average male body mass in this study. We were not able to include the measurements performed by [Ceresoli et al. \(2003\)](#); $26^{\circ} 49' S, 60^{\circ} 25' W$) of two captive giant armadillos, since those measurements do not include body mass. Nevertheless, the measurements provided are generally within the range observed in the present study and in the study of [Silveira et al. \(2009\)](#); [Table B.1](#)).

The variation of body size for males, but not in females, indicates that the degree of sexual dimorphism can vary among localities, which has been documented for other mammalian species (e.g. [Storz et al., 2001](#); [Quin et al., 1996](#)). This also indicates that the two sexes might be subject to different selective forces. The opportunity for sexual selection on male size is expected in species with polygynous mating systems where body mass influences the access of males to receptive females, which seems to be the case for giant armadillos ([Storz et al., 2000](#)). Body size variation can also be related to abiotic factors (e.g. latitude, temperature and topography), differences in productivity among biomes (i.e. resource abundance and distribution), population density, and/or genetic variation between populations ([Francicevic et al., 2005](#); [Pagh et al., 2018](#); [Rodríguez et al., 2008](#); [Storz et al., 2001](#)). The Neotropical region, which encompasses giant armadillo distribution, presents a relatively reduced range of mean annual temperature, when compared to the Nearctic region. In the Neotropics, topography, and not latitude, seems to be the strongest predictor of mammal body size, with the smallest sizes in the high Andes region and the largest sizes in the tropical lowlands and, particularly, in the savannas of Brazil ([Rodríguez et al., 2008](#)). The latitudinal, topographical and climatic range of the giant armadillo studies cover only a part of the species distribution range and present relatively little variation among them. Hence, it is unlikely that the differences observed between the Pantanal and the Cerrado are related to these gradients. To enable this discussion, further information on giant armadillo morphology should be acquired from localities encompassing a broader variation range within the species distribution. However, as large-sized burrowing species that are able to shelter from unfavorable climatic conditions, giant armadillos might not follow the geographical body-size variation pattern expected according to Bergmann's rule ([Medina et al., 2007](#); [Rodríguez et al., 2008](#)). Hence, other factors such as habitat productivity, population density, genetic variation or a combination of them ([Francicevic et al., 2005](#); [Pagh et al., 2018](#); [Rodríguez et al., 2008](#); [Storz et al., 2001](#)) might be responsible for the body mass variation in male giant armadillos and should be explored further in future studies.

While we expected giant armadillo body mass to differ among ecoregions due to varying abiotic conditions, we only encountered variation in male body mass between study sites. This raises interesting ecological questions regarding the relationship between resource availability and body size and how this could be related to the species' reproductive system (e.g. [Storz et al., 2001](#)). However, the number of individuals measured at each study site is small and more individuals should be measured to disentangle individual variation from sexual and population level variation. Furthermore, the study sites do not cover the complete latitudinal/climatic range of the species distribution and other localities along a broader climatic range are needed to verify any broad scale pattern.

Given the unprecedented number of individuals evaluated, in the present study we were able to characterize variations between sexes and age classes, define a subset of morphometric measures that can aid in discriminating these groups, and to gain insights on the species biology and ecology. This is an ongoing project and the long-term monitoring of this population may allow us to understand broader patterns, such as the relationship between body measurements and inter-annual climatic variation or habitat conservation. Finally, we propose that the morphometric measurements protocol used in this study be used as standard measurements for this species since it encompasses all of the most distinctive features of the species and allows a full morphological characterization. The proposed standardization would enable the future comparison between populations of this widely distributed burrowing species and aid the understanding of morphometric variation along its range.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.mambio.2018.12.007>.

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