



An update to the regression to estimate the body mass of extinct xenarthrans

Uma atualização na regressão para estimar a massa corporal de xenartros extintos

M. A. T. Dantas^{1*}; J. P. da Costa²; A. D. S. Soares³; R. E. Fraga⁴

¹Laboratório de Ecologia & Geociências, Universidade Federal da Bahia (IMS/CAT), Campus Anísio Teixeira, 45029-094, Vitória da Conquista, Bahia, Brazil

²Programa de Pós-graduação em Geociências, Faculdade de Geologia, Universidade do Estado do Rio de Janeiro, 20550-013, Rio de Janeiro, Rio de Janeiro, Brazil

³Programa de Pós-graduação em Zoologia, Universidade Estadual de Santa Cruz, 45662-900, Ilhéus, Bahia, Brazil

⁴Laboratório de Biologia Molecular, Universidade Federal da Bahia (IMS/CAT), Campus Anísio Teixeira, 45029-094, Vitória da Conquista, Bahia, Brazil

*matdantas@yahoo.com.br

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In this paper, we provide an update on a regression model designed to estimate the body mass of extinct xenarthrans, particularly those from the Brazilian Intertropical Region. We utilized 84 samples from nine extant xenarthrans species (Pilosa and Cingulata), yielding excellent quality indices ($R^2 = 0.53$, %PE = 4.94, %SEE = 4.44). While there are other good options, we reinforce that this is an excellent tool for estimating the body mass of extinct xenarthrans.

Key words: Xenarthra, ordinary least square, Brazilian Intertropical Region.

No presente trabalho apresentamos uma atualização para uma regressão produzida para estimar a massa corporal de xenartros extintos, em especial os da Região Intertropical Brasileira. Utilizamos 84 amostras de nove espécies viventes de xenartras (Pilosa e Cingulata), alcançando excelentes índices de qualidade ($R^2 = 0,53$, %PE = 4,94, %SEE = 4,44). Apesar de existirem outras ótimas opções, reforçamos que esta é também é uma excelente ferramenta para estimar a massa corporal de xenartros extintos.

Palavras-chave: Xenarthra, mínimos quadrados, Região Intertropical Brasileira.

1. INTRODUCTION

Since 2017, Dantas and collaborators have endeavored to estimate the body mass of extinct xenarthrans from the Brazilian Intertropical Region (BIR) [1]. Initially, they employed allometric regression utilizing the minimum width of the diaphysis of the humerus and femur [2]. A multiple factor in the femur diaphysis were employed in an attempt to determine a more realistic weight for these taxa [1, 3, 4].

Inspired by the regressions proposed by Anderson et al. (1985) [2] and Campione and Evans (2012) [5], a novel method to estimate the body mass of extinct giant sloths and armadillos was proposed using data from extant Xenarthra [6]. Although this new regression exhibited good quality indices, it faced criticism [7, 8], prompting the exploration of additional data to enhance the initial regression. Therefore, the primary objective of this study was to update and justify the utilization of the earlier Xenarthra body mass regression.

2. MATERIAL AND METHODS

We included 79 new samples belonging to extant sloths (*Bradypus torquatus* and *Bradypus variegatus*), anteaters (*Tamandua tetradactyla*, *Myrmecophaga tridactyla*), and armadillos (*Cabassous unicinctus*, *Cabassous tatouay*, *Dasyurus novemcinctus*, *Dasyurus septemcinctus*, and *Euphractus sexcinctus*). In total, the update comprised 84 samples (Table 1). To generate the update, we measured (in millimeter) the circumference at the minimum width of the mid-length (MWM) of the humerus and femoral diaphysis association with the body mass (in grams).

In contrast to previous paper [6], we opted for ordinary least squares (OLS) regression. This choice is based on its superior performance with allometric data compared to the reduced major axis (RMA) [9, 10]. All data underwent logarithmic transformation (base 10). The assessment of the regression quality relied on the correlation of logarithmized data, percent predicted error (% PE) [11, 12], and standard error of the estimate (% SEE) [11].

Table 1. Body mass (in g), humerus and femur circumference (in mm) of extant xenarthran species.

| Xenarthra species | SP# | Humerus Circunference (mm) | Femur Circunference (mm) | Body Mass (g) |
|------------------------------|-----------|----------------------------|--------------------------|---------------|
| <i>Bradypus torquatus</i> | MN 23921 | 27 | 28 | 4200 |
| <i>Bradypus torquatus</i> | UFES 1918 | 39 | 40 | 5500 |
| <i>Bradypus variegatus</i> | UFMG 3988 | 22 | 22 | 750 |
| <i>Bradypus variegatus</i> | UFMG 3987 | 27 | 27 | 1400 |
| <i>Bradypus variegatus</i> | MN 79120 | 25 | 26 | 5000 |
| <i>Bradypus variegatus</i> | MN 79570 | 29 | 30 | 5600 |
| <i>Bradypus variegatus</i> | MN 83742 | 24 | 25 | 6000 |
| <i>Cabassous tatouay</i> | MN 79317 | 37 | 40 | 3100 |
| <i>Cabassous tatouay</i> | MN 4989 | 35 | 31 | 4700 |
| <i>Cabassous unicinctus</i> | LEG 1893 | 28 | 34 | 900 |
| <i>Cabassous unicinctus</i> | LEG 1897 | 25 | 37 | 3000 |
| <i>Choloepus didactylus</i> | ROM 31160 | 40 | 43 | 6200 |
| <i>Choloepus hoffmanni</i> | ROM 89635 | 33 | 35 | 4500 |
| <i>Dasypus novemcinctus</i> | LEG 1890 | 19 | 25 | 283 |
| <i>Dasypus novemcinctus</i> | LEG 1891 | 22 | 29 | 600 |
| <i>Dasypus novemcinctus</i> | MN 4984 | 16 | 27 | 620 |
| <i>Dasypus novemcinctus</i> | LEG 1894 | 18 | 20 | 1000 |
| <i>Dasypus novemcinctus</i> | LEG 1895 | 31 | 37 | 1000 |
| <i>Dasypus novemcinctus</i> | MN 5007 | 19 | 24 | 1090 |
| <i>Dasypus novemcinctus</i> | LEG 1896 | 17 | 23 | 1200 |
| <i>Dasypus novemcinctus</i> | MN 4671 | 17 | 28 | 1750 |
| <i>Dasypus novemcinctus</i> | MN 79546 | 19 | 29 | 2000 |
| <i>Dasypus novemcinctus</i> | MN 79585 | 20 | 31 | 2500 |
| <i>Dasypus novemcinctus</i> | MN 81786 | 20 | 29 | 2500 |
| <i>Dasypus novemcinctus</i> | MN 5008 | 22 | 32 | 2580 |
| <i>Dasypus novemcinctus</i> | MN 4981 | 23 | 32 | 2700 |
| <i>Dasypus novemcinctus</i> | ROM R2385 | 22 | 30 | 3077 |
| <i>Dasypus novemcinctus</i> | MN 5009 | 21 | 30 | 3150 |
| <i>Dasypus novemcinctus</i> | LEG 1898 | 33 | 43 | 3400 |
| <i>Dasypus novemcinctus</i> | MN 79372 | 25 | 31 | 3500 |
| <i>Dasypus novemcinctus</i> | MN 83554 | 21 | 32 | 3500 |
| <i>Dasypus novemcinctus</i> | MN 5006 | 24 | 35 | 3555 |
| <i>Dasypus novemcinctus</i> | MN 4672 | 25 | 35 | 3970 |
| <i>Dasypus novemcinctus</i> | MN 5500 | 30 | 41 | 4000 |
| <i>Dasypus novemcinctus</i> | MN 79456 | 21 | 32 | 4000 |
| <i>Dasypus novemcinctus</i> | MN 79536 | 25 | 40 | 4000 |
| <i>Dasypus septemcinctus</i> | UFES 1217 | 19 | 24 | 510 |
| <i>Dasypus septemcinctus</i> | MN 63454 | 13 | 22 | 670 |

| | | | | |
|--------------------------------|------------|----|----|-------|
| <i>Euphractus sexcinctus</i> | MN 4992 | 31 | 32 | 1680 |
| <i>Euphractus sexcinctus</i> | MN 5000 | 30 | 31 | 2070 |
| <i>Euphractus sexcinctus</i> | MN 4994 | 30 | 28 | 2280 |
| <i>Euphractus sexcinctus</i> | MN 4996 | 27 | 28 | 2280 |
| <i>Euphractus sexcinctus</i> | MN 4976 | 29 | 28 | 2400 |
| <i>Euphractus sexcinctus</i> | MN 5003 | 32 | 35 | 2520 |
| <i>Euphractus sexcinctus</i> | MN 5001 | 30 | 32 | 2560 |
| <i>Euphractus sexcinctus</i> | MN 4998 | 32 | 33 | 2700 |
| <i>Euphractus sexcinctus</i> | MN 4997 | 32 | 34 | 2920 |
| <i>Euphractus sexcinctus</i> | MN 4977 | 33 | 30 | 3030 |
| <i>Euphractus sexcinctus</i> | MN 4999 | 32 | 34 | 3080 |
| <i>Euphractus sexcinctus</i> | MN 4980 | 31 | 32 | 3090 |
| <i>Euphractus sexcinctus</i> | MN 4995 | 34 | 33 | 3340 |
| <i>Euphractus sexcinctus</i> | MN 4986 | 45 | 43 | 4450 |
| <i>Euphractus sexcinctus</i> | MN 4993 | 30 | 33 | 4610 |
| <i>Euphractus sexcinctus</i> | MN 4973 | 34 | 35 | 4700 |
| <i>Euphractus sexcinctus</i> | MN 4979 | 35 | 30 | 5100 |
| <i>Euphractus sexcinctus</i> | MN 4991 | 34 | 35 | 5200 |
| <i>Euphractus sexcinctus</i> | MN 4990 | 31 | 32 | 5250 |
| <i>Euphractus sexcinctus</i> | MN 4982 | 36 | 34 | 5280 |
| <i>Euphractus sexcinctus</i> | MN 5002 | 33 | 34 | 5430 |
| <i>Euphractus sexcinctus</i> | MN 4972 | 35 | 36 | 5500 |
| <i>Euphractus sexcinctus</i> | MN 4988 | 38 | 39 | 5580 |
| <i>Euphractus sexcinctus</i> | MN 4978 | 34 | 35 | 6400 |
| <i>Myrmecophaga tridactyla</i> | MN 5073 | 73 | 71 | 33000 |
| <i>Priodontes maximus</i> | ROM 46260 | 68 | 79 | 29500 |
| <i>Tamandua tetradactyla</i> | LEG 1892 | 34 | 33 | 600 |
| <i>Tamandua tetradactyla</i> | MN 5068 | 32 | 33 | 1110 |
| <i>Tamandua tetradactyla</i> | MN 5069 | 33 | 30 | 2240 |
| <i>Tamandua tetradactyla</i> | MN 4538 | 33 | 32 | 2620 |
| <i>Tamandua tetradactyla</i> | MZFS1159 | 29 | 26 | 3820 |
| <i>Tamandua tetradactyla</i> | UFES 1211 | 45 | 35 | 3875 |
| <i>Tamandua tetradactyla</i> | MN 79361 | 35 | 30 | 4000 |
| <i>Tamandua tetradactyla</i> | MN 83559 | 33 | 32 | 4000 |
| <i>Tamandua tetradactyla</i> | MN 73484 | 32 | 31 | 4250 |
| <i>Tamandua tetradactyla</i> | MN 79209 | 37 | 39 | 4500 |
| <i>Tamandua tetradactyla</i> | MN 79287 | 40 | 32 | 4500 |
| <i>Tamandua tetradactyla</i> | MN 79503 | 33 | 34 | 4570 |
| <i>Tamandua tetradactyla</i> | MN 79564 | 33 | 31 | 5000 |
| <i>Tamandua tetradactyla</i> | MN 79571 | 33 | 30 | 5000 |
| <i>Tamandua tetradactyla</i> | MN 5515 | 33 | 32 | 5070 |
| <i>Tamandua tetradactyla</i> | ROM 113857 | 35 | 30 | 5470 |
| <i>Tamandua tetradactyla</i> | MN 5059 | 38 | 33 | 5500 |
| <i>Tamandua tetradactyla</i> | MN 3846 | 36 | 34 | 5550 |
| <i>Tamandua tetradactyla</i> | MN 5061 | 37 | 39 | 5850 |
| <i>Tamandua tetradactyla</i> | MN 5056 | 39 | 40 | 6670 |

Through the application of an updated regression (see Results and Discussion), we recalculated the body masses of *Eremotherium laurillardi*, *Glossotherium phoenensis*, *Ocnotherium giganteum*, *Catonyx cuvieri*, *Valgipes bucklandi*, *Nothrotherium maquinense*, *Ahytherium aureum*, *Australonyx aquae*, *Pachyarmatherium brasiliense*, *Pampatherium humboldti*, *Holmesina paulacoutoi*, and *Holmesina criptae*.

The majority of the samples were from individuals with either the humerus or femur only. Consequently, the circumference (C) of the missing bone was estimated using the mean proportion between the humerus and femur (f/h) in individuals with partial skeletons containing both bones (Table 2).

Table 2: Proportion between humerus (h) and femur (f) used to estimate the body mass of extinct xenarthrans.

| Taxon | Sample | Circunference (in mm) | | Proportion (f/h) |
|-------------------------|-------------------------|------------------------------|--------------------|-------------------------|
| | | Femur (f) | Humerus (h) | |
| Pampatheriidae | | | | |
| <i>H. paulacoutoi</i> | MCL 501 | 155 | 123 | 1.25 |
| <i>H. criptae</i> | LPP-PV-001 | 126 | 104 | 1.20 |
| <i>P. humboldti</i> | MCL 900 | 148 | 113 | 1.30 |
| Mean value | | | | 1.25 |
| Megatheriidae | | | | |
| <i>E. laurillardi</i> | Port Lavaca, Texas, USA | 532 | 398 | 1.35 |
| <i>N. maquinense</i> | LEG 1454 | 169 | 140 | 1.20 |
| <i>N. maquinense</i> | LEG 1359/1357 | 180 | 154 | 1.15 |
| <i>N. maquinense</i> | MCL 1020 | 125 | 86 | 1.45 |
| Mean value | | | | 1.28 |
| Mylodontidae | | | | |
| <i>G. phoenensis</i> | MCL 4303 | 313 | 210 | 1.50 |
| Scelidotheriidae | | | | |
| <i>C. cuvieri</i> | LEG 1179/1180 | 182 | 150 | 1.20 |
| <i>C. cuvieri</i> | LEG s/n | 370 | 200 | 1.85 |
| <i>V. bucklandi</i> | LEG 1718/1720 | 277 | 175 | 1.60 |
| <i>V. bucklandi</i> | LEG s/n | 210 | 120 | 1.75 |
| Mean value | | | | 1.60 |

The proportion could be determined for individuals described in the literature (*E. laurillardi*, *C. cuvieri*, *H. criptae*) [4, 13, 14]. Alternatively, it could be determined for individuals measured in collections (*N. maquinense*, *V. bucklandi*, *G. phoenensis*, *P. humboldti*, and *H. paulacoutoi*; Table 2). To estimate the body mass we used the mean values of f/h for the families (Table 2). For *P. brasiliense*, *O. giganteum*, and the Megalonychidae taxa were used the proportions found in Pampatheriidae, *G. phoenensis*, and Megatheriidae, respectively.

All studied taxa were categorized as juveniles, subadults, or adults based on the stage of epiphysis–diaphysis fusion in both the humerus and femur. Juveniles exhibit a clear separation between the epiphysis and diaphysis. Subadults display a visible scar between the epiphysis and diaphysis. Adults show complete fusion of both epiphyses to the diaphysis.

3. RESULTS AND DISCUSSION

3.1 Criticism to the earlier regression

The initial criticisms of the Xenartha regression [6, 7] focused on its creation involving the use of only five samples and the estimation of body mass for extinct xenarthrans significantly heavier than those included in the regression. Subsequently, Barbosa et al. (2023) [8] raised new criticisms, suggesting that: (i) the use of the MWM is problematic for estimating the body mass

of extinct xenarthrans; (ii) the database used was phylogenetically restricted; and (iii) the %PE of the original proposition [6] regression was “high”.

Dantas (2022) [6] and Dantas (2022) [15] acknowledges that five samples constitute a low number. Nevertheless, he defends the use of a limited sample size, asserting that the quality indices are moderate (rather than high), considering it a viable option, especially because it was constructed using data from extant Xenarthra. Furthermore, he demonstrated that the circumference and minimum width at the mid-length of the diaphysis are proportional in a sample comprising both extant and extinct xenarthrans. This is supported by the high correlations and similar slopes, suggesting that their volume could also increase proportionally with a strong correlation, which was also observed across all mammals [5].

We observed an overlook criticism regarding the use of MWM to estimate the body mass of extinct xenarthrans [8]. This criticism is directed at the utilization of allometric regressions created using data from non-xenarthrans [16], resulting in an overestimation of body mass. This stimulates the proposition of the development of a specific regression using data from extant xenarthrans [16], which was subsequently implemented [6].

Ultimately, the regression was not phylogenetically restricted; it incorporated data from the focus group [17], which exhibited distinctive humerus and femur morphologies. Consequently, it is a favorable choice for proposing estimations within this specific group of extinct mammals.

3.2. Xenarthra body mass regression updated

The updated regression (1) (Figure 1) exhibited a moderate correlation ($R^2 = 0.53$), low %PE (4.94), and low %SEE (4.44). The correlation was lower than the regression originally proposed [6]. Nevertheless, the %PE and %SEE exhibited excellent values, surpassing those obtained using multiple bones [18, 19].

$$\log_{10}BM = -1.0 + 2.5 * \log_{10}C_{(h+f)} \quad (1)$$

The significant advantage of this regression line is the utilization of one or two bones (humerus and/or femur) from the same individual. This practice prevents the amalgamation of bones from distinct individuals of varying ontogenetic stages and sexes (male/female). The regression facilitates the estimation of body mass of numerous individuals, generating a substantial number of samples. This, in turn, has contributed to a more comprehensive understanding of the body mass variation within these taxa.

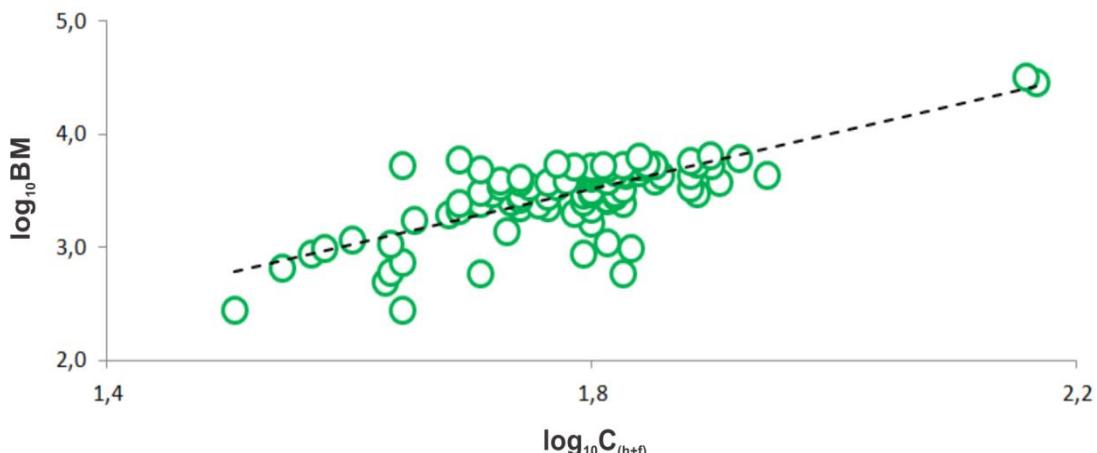


Figure 1: Ordinary least squares of log of body mass (in g) and log of the sum of femur (f) and humerus (h) circumferences (C).

3.3. New xenarthrans body mass estimations for the Late Pleistocene of BIR

Utilizing the updated regression, we proposed new estimations for Late Pleistocene giant sloths and armadillos from the BIR. In Comparison with earlier propositions (Table 3), the body mass of armadillos was similar, except for those proposed elsewhere [8], which, on average, were double our estimations (Table 3).

*Table 3. Mean estimated body mass for adult individuals of 12 xenarthrans taxa (exception to *Ahytherium aureum* and *Catonyx cuvieri*, juvenile - J; and *Au. aquae*, subadult - S) that lived in the late Pleistocene of Brazilian Intertropical Region and comparison with previous estimates.*

| Taxa | Mean±sd (min-max) | Dantas (2022) [6] | Barbosa et al. (2023) [8] method 1 | Barbosa et al. (2023) [8] method 2 |
|-----------------------|-------------------------------|----------------------|---------------------------------------|---------------------------------------|
| <i>P. brasiliense</i> | 68±28 (43-94) | 56 | 89 | 151±5 |
| <i>H. criptae</i> | 80 | 74 | - | - |
| <i>H. paulacoutoi</i> | 94±34 (61-129) | 114 | 176±33 | 194±10 |
| <i>Pa. humboldti</i> | 108 | 98 | 240±55 | 215±103 |
| <i>N. maquinense</i> | 134±64 (57-270) | 157±20 | - | 109±35 |
| <i>A. aureum</i> | 214±29 (172-236) ^J | 186 | - | - |
| <i>Au. aquae</i> | 296 ^S | 226 | - | - |
| <i>V. bucklandi</i> | 703±227 (274-1,065) | 462±127 | 731±120 | 522±193 |
| <i>C. cuvieri</i> | 901±197 (617-1,171) | 598±17 | 776±162 | 558±357 |
| <i>G. phoenensis</i> | 936 | 463 | - | 825±189 |
| <i>O. giganteum</i> | 1,188±300 (837-1,590) | 842 | 1,721±526 | 1,226±282 |
| <i>E. laurillardi</i> | 3,144±1,993 (968-5,969) | 2,014±205 | 4,486±185 | 2,725±1,803 |

Estimates for the giant sloths *N. maquinense*, *A. aureum*, *Au. aquae*, *V. bucklandi*, and *C. cuvieri* were comparable on average (Table 3). Exceptions were noted in previous estimations [6] for *G. phoenensis*, *O. giganteum*, and *E. laurillardi*, which were, on average, ~44% lower than our estimations, but similar to other results [8].

4. FINAL REMARKS

In this paper, we update the Xenarthra regression [6], which now includes 84 samples and excellent indices of quality ($R^2 = 0.53$, %PE = 4.94, %SEE = 4.44). We agree that regression using multiple bones is a good option to propose the body mass of extinct xenarthrans; however, owing to the limitation of complete skeletons, to avoid a general estimation using bones of individuals with ontogenetic stages and sexes, and to have a large number of samples, we reinforce that Dantas' Xenarthra regression is a viable and excellent option.

Finally, we updated the body mass estimations made for giant sloths and armadillos in the Brazilian Intertropical Region.

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