

# Limb bone stress in the mara *Dolichotis patagonum* (Caviomorpha; Caviidae; Dolichotinae)

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**Type**

Research paper

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**Keywords**

body posture, Tibia, locomotion, Rodentia, mammal gait

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**Abstract**

Abstract.- The mara *Dolichotis patagonum* (Caviomorpha, Caviidae) is probably the extant rodent with the most pronounced postcranial specializations for fast locomotion. When running the species can reach a speed of ~40 km/h. It has been suggested that its body posture and limb bones show evolutionary parallelism regarding small-sized artiodactyl species. Due to its elongated limbs and relatively large body mass (average 8 kg) compared to other rodents, its limb bones may experience large loads at high speeds. Using kinematic data from high speed video films and skeletal dimensions of museum specimens, ground reaction forces and stresses acting on the humerus and tibia during different gaits were estimated. Values of bending stress obtained for the tibia were greater than those for the humerus during walking, gallop and “pronk”. The stress experienced by the tibia when running doubled the value obtained when walking (54.5 vs. 26.1 MPa, respectively). Estimated bone safety factors were less than half during fast locomotion (3.1) compared to walking (6.4). It is discussed how maras’ body posture and skeletal dimensions affect bone stress experienced during locomotion.

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**Explanation letter**

Mar del Plata, 25 March 2020

Dr. Lucas A Wauters  
Editor of Hystrix

Please, find attached the revised version of the manuscript entitled “Limb bone stress in the mara *Dolichotis patagonum* (Caviomorpha; Caviidae; Dolichotinae) “to be considered for publication in Hystrix, the Italian Journal of Mammalogy.

The comments made by both reviewers were taken into account in this revised version. Please find below a detailed response to each comment/suggestion.

Looking forward to hearing from you

Sincerely yours

Prof. Dr. Aldo Iván Vassallo  
Universidad Nacional de Mar del Plata

Review 1:  
Limb bone stress in the mara *Dolichotis patagonium*.

This manuscript examines the loads borne by the humerus and tibia of the mara.

I do not find any errors in the analyses, but the manuscript lacks a question or hypothesis. Perhaps that hypothesis could be that the mara is expected to show similar values of limb bone stress in different types of locomotion as small artiodactyls, and to be quite dissimilar to small cursorial rodents.

Response: The main study question and hypothesis were added at the end of the Introduction.

The following are some suggestions to improve the English and a request for better justification of the 4:6.- forelimb: hindlimb loading ratio.

Page 2 line 11 replace “efforts” with “loads”

Page 3 line 37 remove “among other traits” unless you plan to mention them.

Page 4 line 57 replace “efforts” with “loads”

Page 4 line 67 and page 5 line 79 the use of the word “physiognomy” is potentially problematic because although it can mean ‘the general appearance of something’ it is most often associated with the pseudoscience of reading character from human facial features. I suggest the word “structure” or “body form”

Page 5 line 99 – gastrocnemius is described as a foot “extensor”. I know this is debatable and many would argue that it is the correct word, but I would be happier if the term “plantarflexor” was used.

Page 6 line 102 “... when the glenoid fossa passes over the hand,” I would suggest “hand contact”

Page 6 line 104 similarly with “foot contact”. The hand and especially the foot are quite large and adding the word “contact” describes a more specific and correct location.

Response: We agree with the above reviewer's suggestions regarding grammar, names of anatomical structures, and other clarifications; we made the requested corrections.

Page 6 line 114 “...Given the relatively greater development of the hind limbs, it was assumed that they support 0.6 of the body weight, and the forelimbs 0.4.” This is a bit circular! There should be a reference for this as generally in quadrupeds the forelimb supports more of the body weight than the hind limbs. Perhaps there is data about the forelimb versus hindlimb load distribution in small ungulates. This is important because the results of the analyses (Values of bending stress obtained for the tibia were greater than those for the humerus in all gaits..) depend heavily on this proportion.

Response: We agree with the reviewer that the proportion of body weight supported by the fore and hind legs strongly influences our estimates of bone stress. Unfortunately, we have found no published studies about the forelimb versus hindlimb load distribution in mammals comparable to the mara. Accordingly, and for the reasons stated in the revised version of the manuscript, we adopted in this version a conservative assumption of equal body weight support (0.5) by fore and hind limbs. The stress values varied a bit, so we corrected values in Table 1, but the general interpretation of the results remains.

Page 9 line 175 replace “greatest” with “greater” (only two things are being compared)

Page 9 line 176 “medial limb bones” surely you mean distal... Yes I know that the metatarsals and meta carpals are the most distal but medial is still not the right word. Perhaps you want to call the tibia radius and ulna the “intermediate limb bones”. However as you are not examining the stresses in the more distal elements, I think “distal” would be ok

Page 9 line 189 replace “what” with “than”

Line 190 delete “, the authors say”

Page 10 line 207 replace “efforts” with “loads”

Page 11 lines 237 to 239 I suggest rewriting the sentence as follows “ The safety factor helps characterise the relationship between the maximum stress ( ) that the bone is able to endure and the stresses that are confronted by the organism during real performance in nature.”

Page 12 line 253 replace “regarding” with “and”

Response: We agree with the above suggestions of the reviewer; the requested corrections were made.

Review 2:

The work deal with an estimation of the limb bone stress in the mara. The particular locomotor behaviour of such species makes very interesting the matter. In fact, the mara, while pertaining to an order of generally non-cursorial mammals, presents the morphological and functional characteristics of cursoriality.

I will put down some criticism of the paper, with the purpose to improve it.

Introduction:

Row #53 to #55: I don't understand this sentence. Could you clarify?

Response: We hope that this sentence, as written in the revised version, became clearer.

Row #58: Safety factor. I will write more on this point later. In the introduction it should be advisable to explain a little more what it is and why is it important.

Response: In the revised version, the term safety factor and its structural implication were explained in the Introduction section.

Results:

It is not clear how the Safety Factor (SF), presented in results (table 1), was computed.

We need to reach the row #239 in discussion to understand that the SF was calculated after two values of bone strength taken from a book (Table 9.1 in Currey, 2006).

Response: In the revised version, a paragraph was added in Materials and Methods explaining how the safety factor was calculated.

Firstable, also because a book is less accessible than an article (as far as I know, Currey “Bones” is not available for download), I would ask to put the values of bone yield strength taken as reference in materials and methods, with the calculation formula of SF.

Response: bone strength values taken as a reference and the calculation formula of SF were included in M&M.

Second: in table 10.4 of the same reference (Currey, 2006), the SF of various bones was computed assuming yield strengths of 172 MPa (tension) and 284 Mpa (compression), slightly different from 150 MPa and 250 MPa presented in table 9.1. Why did you choose the latter?

Response: We use the values in Currey's Table 9.1 (instead of yield strength as in Table 10.4) because they are ultimate bone strength values. Thus, our safety factors were based on the maximum stress that the bone can sustain before fracture, what we think has a greater biological meaning than the loss of its elastic response.

Limb bone stress in the mara *Dolichotis patagonum* (Caviomorpha; Caviidae;  
Dolichotinae)

A running title: Limb bone stress in the mara

Abstract.- The mara *Dolichotis patagonum* (Caviomorpha, Caviidae) is probably the extant rodent with the most pronounced postcranial specializations for fast locomotion. When running the species can reach a speed of ~40 km/h. It has been suggested that its body posture and limb bones show evolutionary parallelism regarding small-sized artiodactyl species. Due to its elongated limbs and relatively large body mass (average 8 kg) compared to other rodents, its limb bones may experience large loads at high speeds. Using kinematic data from high speed video films and skeletal dimensions of museum specimens, ground reaction forces and stresses acting on the humerus and tibia during different gaits were estimated. Values of bending stress obtained for the tibia were greater than those for the humerus during walking, gallop and “pronk”. The stress experienced by the tibia when running doubled the value obtained when walking (54.5 vs. 26.1 MPa, respectively). Estimated bone safety factors were less than half during fast locomotion (3.1) compared to walking (6.4). It is discussed how maras’ body posture and skeletal dimensions affect bone stress experienced during locomotion.

Key words: locomotion – body posture – mammal gait – tibia - Rodentia

## INTRODUCTION

Limb bones must be able to withstand loadings resulting from muscle activity and ground reaction forces (GRF), i.e. the forces exerted by the ground upon the animal body, whether it is stationary or moving. The GRF varies depending on the particular type of gait being performed by the animal (walking, galloping, running), reaching high values during

fast locomotion (Alexander 2003). Since these forces are concentrated in places such as sites of muscle origin and insertion, and sites of contact between bones (e.g. joints), it is assumed that they exert force per unit area which is called stress and usually expressed in MPa (megapascals, i.e. newton per square millimeter). Peak GRF acting on a single limb are usually less than body weight when an animal moves slowly, but it might be much greater than the animal weight during fast locomotion (Biewener 1990, Alexander et al. 1979). For example, it was found that the vertical GRF on a leg increases linearly during walking and running from 1.2 bw at 1.5 m s<sup>-1</sup> to 2.5 bw at 6 m s<sup>-1</sup> (Keller et al. 1996).

In mammals, typical morphological adaptations to increase speed include limb lengthening—especially of its distal segments—, upright stance, unguligrade or digitigrade foot posture, and limb muscles attachments placed near the joints (Hildebrand and Goslow 2005, Feldhamer et al. 1999). An elongated limb can perform a long stride, which together with the increase in the frequency of the gait cycle results in high speeds (Loguercio 2009, Hildebrand 1989). In turn, at high speeds the GRF also increase which impacts upon the mechanical stress that the limb bones must withstand (e.g. Witte et al. 2004). Another issue to take into account when assessing bone stress is the angle between the limb segments with respect to the direction of the GRF vector. This angle might change according to speed and the type of gait being performed by the animal (Day and Jayne 2007, Rocha-Barbosa et al. 2005, Goslow et al. 1973). For this reason, limb bones will be subjected to varying axial (i.e. parallel to main axis) and bending (i.e. perpendicular to main axis) stresses.

Limb bone morphology is extremely variable in terrestrial mammals, adapting to mechanical demands imposed by the different locomotion modes, and also to species body mass (Morgan 2009, Cubo et al. 2008, Alexander 2003, Christiansen 2002). In those few species where data have been collected, it has been estimated that the incidence of long

bone fractures is not negligible, varying between 0.4-6% (Currey 2006, Brandwood et al. 1986). Since fractures may cause a substantial detriment to survival and reproductive success, it is of interest to make estimates of the stresses to which the long bones are subjected during locomotion. This is particularly relevant in cursorial species where fast locomotion might produce peak loads, for example when escaping from predators. To address this point, and to characterize bone strength, the concept of safety factor is often useful (Alexander 1996, Currey 2006). In engineering practice, the safety factor of a structure is the ratio of its failure strength to the maximum stress that it must confront in a real situation. The concept was coopted by animal biomechanics to characterize the margin of safety present in skeletal structures (Alexander 1981).

Caviomorph rodents constitute a monophyletic group of South American mammals (Upham and Patterson 2012) that have diversified into different habitats, occupying jungles of the tropical and subtropical regions of the northern continent, as well as open environments of its southern portion (Vassallo and Antenucci 2015). For this reason, the different clades have evolved different locomotion modes and habits, which include climbing, digging, cursorial locomotion, swimming, which are reflected in several postcranial specializations (Candela et al. 2017, Morgan 2015). While certain species of caviomorph rodents show the typical rodentiform body form, characterized by relatively short legs and a crouched body posture (e.g. *Thrichomys apereoides*; *Cavia aperea*; *Galea musteloides*; *Ctenomys sp.*) others have evolved a set of features convergent with cursorial artiodactyls (Rocha-Barbosa et al. 2015, Osbahr et al. 2009). For example, the mara *Dolichotis patagonum*, Zimmermann, 1780 (body mass range: 7.7 – 8.3 kg) is probably the extant rodent with the most pronounced postcranial specializations for cursoriality (Alvarez et al. 2013, Elissamburu and Vizcaíno 2004, Campos et al. 2001), most likely as an

adaptation for predation avoidance. Maras inhabit open environments in southern South America co-occurring with cursorial carnivores such as pumas and culpeo foxes, two species that prey on it (Zanón Martínez et al. 2012). Maras have a slender body and the longest limbs amongst caviomorph rodents (Elissamburu and Vizcaíno 2004). The tibia and the metatarsals are particularly elongated. Given this particular body form, and the fact that the species is capable of running at speeds similar to those achieved by species of small-sized artiodactyls (Chagas et al. 2019), the present study investigates how limb bone stress in different types of locomotion compares with that experienced by species of artiodactyls and other cursorial mammals. Because of its upright posture the mara is expected to show bone stress values comparable to that of small sized rodents.

## MATERIALS AND METHODS

The kinematic parameters necessary to estimate ground reaction forces, and limb bones angle with respect to the vertical were measured from high-speed videos (300-600 fps) taken with a Casio Exilim EX-F1 digital camera on 10 adult individuals of *Dolichotis patagonum* housed in the Zoo of Batán (Buenos Aires Province). The methodology used to record the videos was detailed in Chagas et al. (2019). Duty factors (i.e. the percentage of the locomotor cycle in which a given limb is resting on the ground) when performing different gaits were taken from Chagas et al. (2019).

Morphological variables of the humerus and tibia used to estimate their cross-sectional area at mid-shaft were taken on four adult specimens (MLP: 642; 275; 208; 250) housed at the Mammalogy Collection of La Plata Museum, Argentina. The medio lateral and antero posterior diameters of bone marrow cavity and external periosteal surface were measured at half the length of the humerus and tibia shaft from x-rays taken at Instituto Radiológico



(Mar del Plata). Values measured on left and right bones were averaged for the cross-section calculation. For bone stress estimations (see below) the four specimens were averaged. Mean olecranon length (lever arm of the triceps, a forearm extensor muscle) was 26.74 mm; mean calcaneus length (lever arm of the muscle gastrocnemius, a plantar flexor) was 26.76 mm. Mean metatarsal length was 112.91 mm. The angles of the humerus and ulna with respect to the vertical at the moment when the glenoid fossa passes over the hand contact, and the angles of the tibia and metatarsals with respect to the vertical at the moment when the acetabulum passes over the foot contact were measured as shown in Fig. 1. These are the moments, during the gait cycle support phases of fore and hind limb respectively, when GRF reaches its maximum (peak) value, acting closely with respect to the vertical (Biewener 1990, Alexander 1977). The angles were measured for the different gaits performed by maras from selected video film frames. 8 kg (both sexes averaged) was taken as the body mass of adult maras (Campos et al. 2001). The angles of the triceps muscle with respect to the humerus, and the gastrocnemius with respect to the tibia were estimated from the analysis of a complete skeleton of an adult mara prepared in the Laboratorio de Morfología Funcional y Comportamiento (Universidad Nacional de Mar del Plata; IIMyC). These angles were  $8^\circ$  and  $0^\circ$ , respectively. Estimates of bone stress depend on assumptions about proportion of body weight supported by fore and hind limbs. Since in quadrupeds the head and neck tend to shift the center of mass of the body cranially, generally the fore limbs support more of the body weight than the hind limbs. Yet, the size and mass of the appendicular system may also influence the location of the center of mass (Druelle et al. 2019). Given the greater development of the posterior trunk and limbs in maras, which may compensate the effect of the head and neck, we adopt here a conservative assumption of equal body weight support (0.5) by fore and hind limbs. GRF

and bone stresses were estimated for the following gaits: walking, gallop, half bound, and pronking, as defined by Hildebrand and Goslow (2005) and Chagas et al. (2019). The methodology follows Alexander et al. (1979); it is exemplified by the calculations made for the tibia during walking. The same procedure was used in the other gaits for the humerus and tibia.

The peak ground reaction force was estimated as:

$$[1] \text{ GRF on a limb} = \text{supported fraction of body weight} \cdot \text{body mass} \cdot \text{acceleration of gravity} \cdot 1 / \text{duty factor} \cdot \pi / 2$$

$$\text{GRF on both fore and hind limb, walking} = (0.25 \cdot 8 \cdot 9.81) \cdot (1 / 0.64) \cdot (3.1416 / 2) = 48.32 \text{ N}$$

For the other gaits their corresponding duty factors (Table 1) were used.

The axial and perpendicular components of GRF acting on the tibia in a walking mara were calculated as follow:

$$[2] \text{ GRF}_{\text{axial}} = \text{GRF on hind limb} \cdot \cos(\text{angle of the tibia with respect to the vertical})$$

$$\text{GRF}_{\text{axial}} = 48.32\text{N} \cdot \cos 0.70 = 37.07 \text{ N}$$

The axial component of muscle force (MF) on the tibia is:

$$[3] \text{ MF}_{\text{axial}} = \text{MF} \cdot \cos(\text{extensor muscle angle with respect to the tibia}) = \text{GRF on the tibia} \cdot \text{Moment Arm}_{\text{GRF}} / \text{Moment Arm}_{\text{extensor muscle}}$$

$$\text{Moment Arm}_{\text{GRF}} = \text{metatarsal length} \cdot \sin(\text{metatarsal angle to vertical}) \text{ (see Fig. 2)}$$

$$\text{MF}_{\text{axial}} = 48.32\text{N} \cdot (112.9\text{mm} \cdot \sin 0.69 / 26.7\text{mm}) = 130.24 \text{ N}$$

The net axial force on the tibia is:

$$[4] \text{ F}_{\text{axial}} = \text{GRF}_{\text{axial}} + \text{MF}_{\text{axial}} = 167.32 \text{ N}$$

The compression stress (CS) due to axial force is:

[5] CSaxial = Faxial / cross-sectional area of the long bone

$$CS_{axial} = 167.32 \text{ N} / 61.51 \text{ mm}^2 = 2.72 \text{ MPa}$$

The cross-sectional area of the tibia CST was estimated by assuming a hollow ellipse as:

$$CST = \pi / 4 [(D_{ap} \text{ external antero-postero diameter} \cdot D_{lm} \text{ external latero-medial diameter}) - (d_{ap} \text{ internal antero-posterior diameter} \cdot d_{lm} \text{ internal latero-medial diameter})] = 61.51 \text{ mm}^2$$

Where  $D_{ap}=10.18 \text{ mm}$ ;  $D_{lm}=10.68 \text{ mm}$ ;  $d_{ap}=5.49 \text{ mm}$ ;  $d_{lm}=5.63 \text{ mm}$

The perpendicular component of the GRF on the tibia is:

$$[6] GRF_{perp} = GRF \text{ on the hindlimb} \cdot \sin (\text{angle of the tibia to the vertical})$$

$$GRF_{perp} = 48.32 \text{ N} \cdot \sin 0.70 = 31.00 \text{ N}$$

The perpendicular component of muscle force on the tibia is:

$$[7] MF_{perp} = \sin (\text{angle of extensor muscle with respect to the bone}) \cdot GRF \text{ on the hindlimb} \cdot \text{Moment Arm}_{GRF} / \text{Moment Arm}_{\text{extensor muscle}}$$

$$FM_{perp} = \sin 0 \cdot 48.32 \text{ N} \cdot (112.91 \text{ mm} \cdot \sin 0.69 / 26.76 \text{ mm}) = 0$$

Net perpendicular force on the tibia is  $F_{perp} = GRF_{perp} + MF_{perp} = 31.00 \text{ N}$

The bending stress (BS) on the tibia mid-shaft due to  $F_{perp}$  (e.g. Ozkaya and Nordin 1999) is:

$$[8] BS = M \cdot y / I$$

Where  $M$  is the bending moment;  $y$  is the vertical distance between the tibia neutral axis and the point at which the stress is sought, and  $I$  is the second moment of area of a hollow ellipse,  $\pi (D_{ap}^3 \cdot D_{lm} - d_{ap}^3 \cdot d_{lm})/64$

$$BS = 31.00 \text{ N} \cdot 32 \cdot (84 \text{ mm}) \cdot D_{ap} / (\pi (D_{ap}^3 \cdot D_{lm} - d_{ap}^3 \cdot d_{lm})) = 26.14 \text{ MPa}$$

$$\text{Net tensile stress on the tibia} = BS - CS_{axial} = 23.42 \text{ MPa}$$

$$\text{Net compression stress on the tibia} = BS + CS_{axial} = 28.86 \text{ MPa}$$

Safety factors were calculated as the quotient between bone strength divided by stress values at bone midshaft which were estimated for the different gaits. Average values of bone strength taken from the literature (150 MPa in tension; 250 MPa in compression; Table 9.1, Currey 2006) were used since at the moment there are no specific studies on the mechanical properties of maras's limb bone.

## RESULTS

Estimated ground reaction force on both the hindlimb and forelimb increases from 0.62 body weight during walking to 1.19 body weight during running (half bound). Values of bending stress obtained for the tibia were greater than those for the humerus during walking, gallop and "pronk" (Table 1). Based upon bone ultimate tensile strength of 250 and 150 MPa under compression and tension, respectively (Currey 2006), it was found that tibia and humerus bone safety factor decreased to less than half when the mara passes from walking to galloping or running (Table 1).

## DISCUSSION

The relatively high bending stresses supported by the tibia during walking, gallop and “pronk” most likely result from of its greater functional length with respect to the humerus. As in other cursorial mammals, the mara shows proportionally longer distal limb bones -- tibia, radius and ulna-- with respect to proximal ones, femur and humerus (Hildebrand and Goslow 2005, Pike and Alexander 2002). The average functional length of the tibia in the specimens analyzed, 168 mm, was ~60 % greater than that of the humerus, 105 mm, so the bending moment produced by the perpendicular component of the GRF at the tibia mid-shaft was greater. Another factor that can affect bending stress is the angle of the long bone with respect to the vertical, which may explain the greater value obtained for the humerus during half bound, a gait during which this bone shows a greater angle than the tibia. A greater bending stress supported by the tibia cannot be attributed to the fact that this bone has a smaller cross-sectional area with respect to the humerus since the opposite is valid. The cortical bone cross-sectional area at the humerus mid-shaft was 52.46 mm<sup>2</sup> (N=4; SD 9.34) whereas for the tibia this value was 61.51 mm<sup>2</sup> (N=4; SD 13.80). The greater cortical bone cross-sectional area of the tibia as compared to the humerus agrees with the fact that in mammals, in general, the hind limbs generate a relatively greater impulse (Walter and Carrier 2007, Bryant et al. 1987) therefore their bones should be more robust. In line with this, Hudson et al. (2011) found that the cheetahs’ femur and tibia had a larger mid-shaft diameter, what would be necessary to maintain the bones’ strength and safety factors with increasing limb bone length.

A comparative study on long bone proportions in rodents and insectivores having different locomotion modes and body masses (Bou et al. 1987) showed that the mara has

213 relatively elongated fore and hind limbs, especially due to the lengthening of the tibia and  
214 ulna. This condition, which allows performing long strides, is associated with the relatively  
215 higher speeds that this species can reach compared to other rodents (Chagas et al. 2019).  
216 Ellissamburu and Vizcaino (2004) analyzed morphological characteristics of the limbs  
217 focusing on caviomorph rodent species having different locomotion modes, body mass, and  
218 habitat. From linear variables measured on fore and hind-limb bones these authors  
219 calculated functional indices to assess species morphological adaptations. They found that  
220 the tibia robustness index, a bone strength indicator calculated as its transverse diameter at  
221 mid-shaft divided by its functional length, was not substantially lower in the mara when  
222 compared to the values obtained in non cursorial relatively short-limbed species such as  
223 *Galea* and *Chinchilla* (Table 2 in Ellissamburu and Vizcaino 2004). This suggests that  
224 although maras' hind limbs are proportionally longer than in other rodent species, mainly  
225 due to its long tibia, it is also true that this bone has experienced an increase in its diameter,  
226 which is probably related with the loads it must bear during fast locomotion.

227 Estimates of GRF when galloping, running and pronking roughly doubled those  
228 estimated for walking. Consequently, the net tensile and compressive stresses on the tibia  
229 and humerus during fast gaits are also doubled as compared to walking. These stresses are  
230 within the same order of magnitude as those estimated by Alexander et al. (1979) for  
231 mammalian species having body masses as different as dog, buffalo and kangaroo, when  
232 they run or jump. In the buffalo, the dog and the mara tensile and compressive stress values  
233 overlap partially, belonging to the same order of magnitude (Table 2), yet their body  
234 masses differ in one and two orders of magnitude. This fact suggests that the stresses  
235 experienced by limb bones during locomotion are rather similar in animals that differ

237 markedly in body mass as previously proposed by Biewener (1990, 1983) and Currey  
238 (2006).

239 Another factor that could affect bending stresses during fast locomotion is body posture,  
240 which may vary during the different gaits. If the angle of limb bones with respect to the  
241 vertical is greater, the greater is the component of the peak GRF that generates bending  
242 moment, i.e. the component perpendicular to the longitudinal bone axis. As showed in  
243 Table 1, the angle of the tibia, as well as that of the humerus, were greater when galloping  
244 and running as compared to walking, which partly explains the greater bending stress  
245 estimated during fast locomotion in maras. However, the mara adopts a relatively upright  
246 posture as compared to the typical crouched body posture of rodents in general (Fig. 3).  
247 Thus, while the angle of the humerus with respect to the vertical in a galloping mara is 46.5  
248 ° (Table 1), this angle is ~56 ° in the humerus of the rodent *Cavia* moving with the same  
249 gait, as can be estimated from Fig. 2 in Rocha Barbosa et al. (2005). Both species belong to  
250 the family Caviidae, but while mara body mass might exceed 8 kg, that of *Cavia* rarely  
251 exceeds 900 g. Having a relatively large body mass, maras's body posture could alleviate  
252 scaling effects upon muscle supporting forces and bone stress. Biewener (1989) argues that  
253 the upright posture adopted by animals with greater body mass, by "aligning" the limb  
254 bones with respect to the peak GRF, allows reducing both the force that the muscles must  
255 exert to support the animal as well as the compressive stress that the limb bones must resist.

256 The safety factor helps characterize the relationship between the maximum stress (i.e.,  
257 force per unit area) that the bone is able to endure and the stresses that are confronted by  
258 the organism during real performance in nature. The range of safety factor, 3-5.3 during the  
259 fastest gaits (Table 1), was similar to that found in other mammalian species, of similar or

261 even greater body mass (Biewener 1982, Alexander 1981). Safety factors calculated for the  
262 tibia were in general lower than those in the humerus which agrees with the greater stress  
263 experienced by the hind limb bone. It has been suggested that the stress experienced by  
264 limb bones, and their corresponding safety factors, are determinant of the athletic ability  
265 (e.g., maximum running speed, maneuverability at fast gaits, coordination) of terrestrial  
266 vertebrates, which is relevant when assessing predator-prey relationships (Sorking 2008).

267 It has been proposed that there is an evolutionary parallelism in long bones morphology  
268 and locomotion between some cursorial rodent species such as *Cuniculus paca*, *Dasyprocta*  
269 *leporina* and *Myoprocta acouchy* and small sized artiodactyl species such as *Tragulus*  
270 *javanicus* (Rocha-Barbosa et al. 2015, Rocha-Barbosa and Casinos 2011). When analyzing  
271 several parameters that define the biomechanical performance of limb bones such as their  
272 cross-sectional area, second moment of inertia, and other indicators of athletic ability these  
273 authors found no significant differences between a sample constituted by several species of  
274 cavioid rodents as compared to species of artiodactyls. Is the stress experienced by the limb  
275 bones of cursorial rodents and artiodactyls similar? For a 70 kg antelope galloping at  
276 maximum speed Alexander (1977) estimated bending stresses on the humerus and tibia of  
277 140 and 150 MPa, respectively. In the present study on mara, during the fastest locomotion  
278 (“half bounding”), these stresses were estimated at 57.2 and 54.5 MPa for the humerus and  
279 tibia, respectively (Table 1), less than half of the antelope’s values. Since both studies used  
280 the same procedure to estimate bone stress, based upon kinematic data, skeletal dimensions  
281 and similar assumptions, these differences could be due to the lower duty factors measured  
282 in the antelope (0.18-0.20) compared to that of maras (0.33; Table 1), most likely due to  
283 the relatively higher speed achieved by the artiodactyl species.



Locomotor behavior has profound effects on the stress experienced by the skeleton, so it constitutes a source of selection pressure on the anatomy of bones and body posture. Cavimorph rodents have evolved highly diverse limbs in terms of their shape and segment proportion, from relatively short and robust limbs capable of withstanding large efforts in digging and climbing species (Candela and Picasso 2008, Lessa et al. 2008), to elongated and graceful limbs in cursorial species (Sundaram et al. 2017). Maras clearly depart from rodent's body form and locomotion (e.g. Samuels and Van Valkenburgh 2008) showing some morphological parallelism with artiodactyls. Despite the high speeds that maras can reach, and its relatively large size, the stresses experienced by its limb bones are rather similar to those recorded in small sized rodents. This fact is most likely related to his upright posture and the robustness of the tibia.

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Table 1 Ground reaction force (GRF), bone stress, and safety factors estimated during different gaits performed by the mara *Dolichotis patagonum*. \* from Chagas et al. 2019

	lateral walk		gallop		half bound		“prnk”	
Speed (m/s)*	1.16		6.10		8.95		3.02	
Duty factor *	0.64		0.37		0.33		0.29	
	hind and forelimb		hind and forelimb		hind and forelimb		hind and forelimb	
GRF (N)	48.32		83.66		93.30		105.80	
GRF % body weight	0.62		1.07		1.19		1.35	
	tibia	humerus	tibia	humerus	tibia	humerus	tibia	humerus
Angle to vertical	39.9°	35.2°	49.7°	46.5°	43.8°	51.6°	31.0°	34.5°
Bending stress (MPa)	26.14	18.24	53.82	42.17	54.51	57.22	46.03	42.29
Net tensile stress (MPa)	23.42	16.16	49.06	37.48	48.58	49.98	39.76	36.91
Net compressive stress (MPa)	28.86	20.33	58.57	46.87	60.45	64.46	52.30	47.68
Tensile safety factor	6.40	9.28	3.06	4.00	3.08	3.00	3.77	4.06
Compressive safety factor	8.66	12.30	4.27	5.33	4.13	3.88	4.78	5.24

Table 2 Bone stress during fast locomotion in mammal species of different sizes. From Alexander 1977, Alexander et al. 1979, Biewener 1983, and the present study.

Species	Gait	Mass (kg)	Tensile stress (MPa)		Compressive stress (MPa)	
			humerus	tibia	humerus	tibia
buffalo	gallop	500	93	36	113	58
elephant	fast locomotion	2500	69	45	85	57
wallaby ( <i>Protemnodon</i> )	hopping	11		65		90
dog	jumping	26	80	60	80	100
antelope	gallop	70	150	126	150	154
ground squirrel	gallop	0.11-0.14	28.7	47.2	30.2	65.8
chipmunk	gallop	0.92-0.96	33	43.8	41.2	57.5
mara	gallop	8	37.5	49.1	46.9	58.6



## FIGURES AND LEGENDS

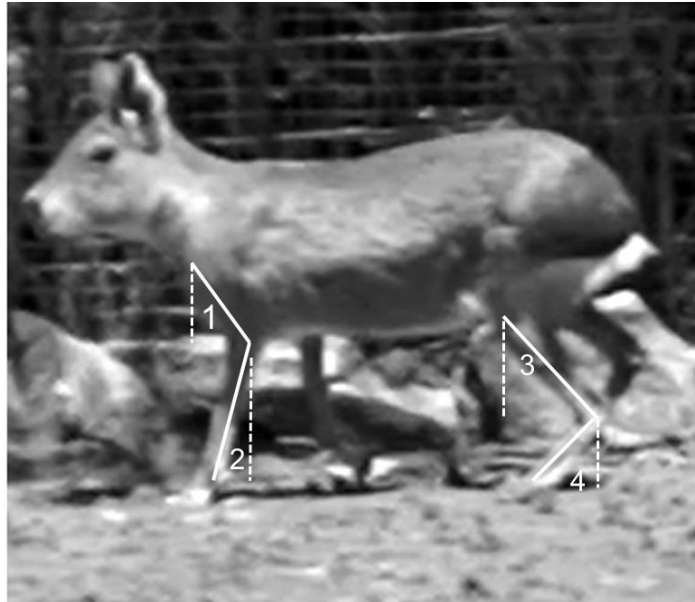
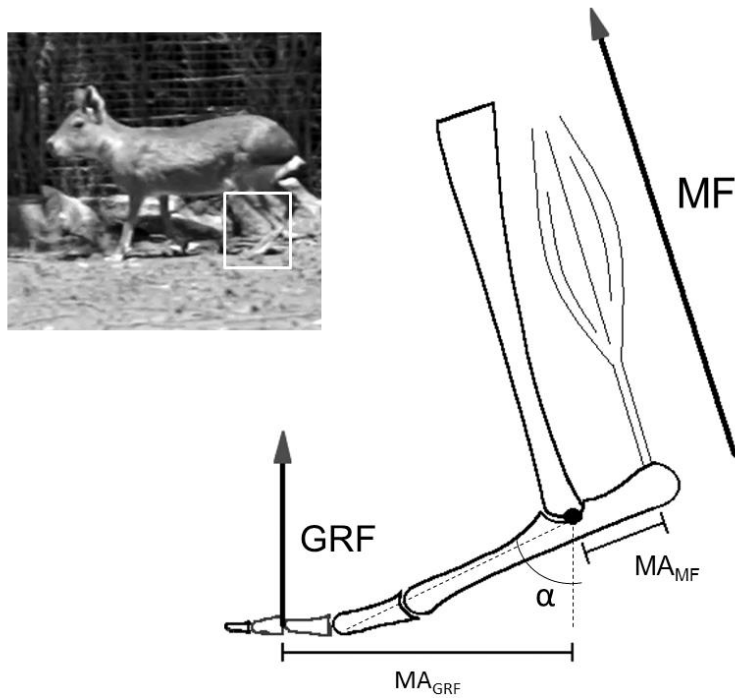


Fig. 1 Angles of the humerus (1) and ulna (2) with respect to the vertical (broken line) at the moment when the glenoid fossa passes over the hand contact, and angles of the tibia (3) and metatarsals (4) with respect to the vertical at the moment when the acetabulum passes over the foot contact. These are the moments, during the gait cycle support phase, when the ground reaction force was assumed to reach its maximum value (Alexander, 1977). Adult walking mara, image captured from a high-speed video film.



474 Fig. 2 Estimation of the ground reaction force moment arm ( $MA_{GRF}$ ) acting on the tibia -  
475 metatarsal joint (Biewener 2003).  $MA_{GRF}$  = metatarsal length  $\cdot$   $\sin \alpha$  (metatarsal angle to  
476 vertical).  $MA_{MF}$ : extensor muscle moment arm; GRF: ground reaction force vector; MF:  
477 extensor muscle force vector. Insert: walking mara photo captured from a high-speed video  
478 film.



480 Fig. 3 Crouched body and plantigrade posture in short-limbed cuis *Cavia apera* (above,  
481 photo by C. D. Timm) vs. upright body and digitigrade posture in the mara *Dolichotis*  
482 *patagonum* (below, photo taken from Wikimedia Commons). Both species belong to the  
483 family Caviidae (Rodentia, Caviomorpha).

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