Research Article

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

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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.

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 $1.5\,\mathrm{m\,s^{-1}}$ to 2.5 bw at $6\,\mathrm{m\,s^{-1}}$ (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

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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 kg–8.3 kg) is probably the extant rodent with the most pronounced postcranial specializations for cursoriality (Álvarez 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. Eight 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° and 0°, 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 craneally, 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 conser-
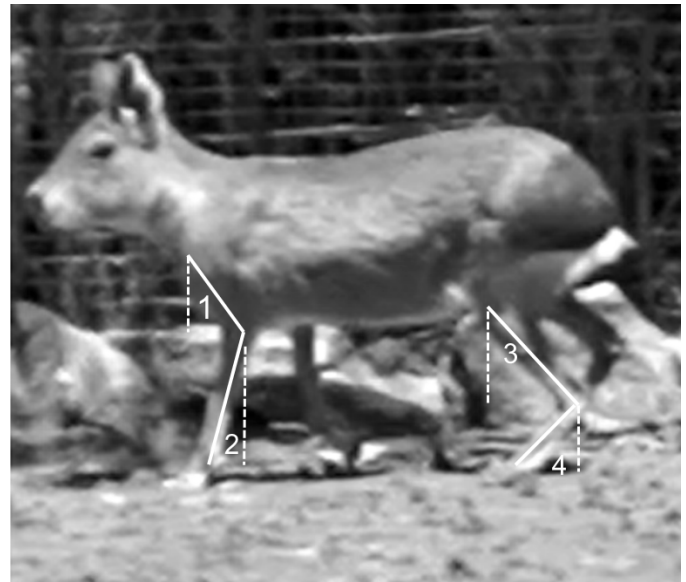
Figure 1 – Angles of the humerus (1) and ulna (2) with respect to the vertical (broken line) at the moment when the glenoid fossa passes over the hand contact, and angles of the tibia (3) and metatarsals (4) with respect to the vertical at the moment when the acetabulum passes over the foot contact. 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.

vative assumption of equal body weigh 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] GRF on a limb = supported fraction of body weight · body mass · acceleration of gravity · $1/$ duty factor · $\pi/2$. GRF on both fore and hind limb, walking = $0.25 \cdot 8 \cdot 9.81 \cdot 1/0.64 \cdot \pi/2 = 48.32$ N. For the other gaits their corresponding duty factors (Tab. 1) were used.

The axial and perpendicular components of GRF acting on the tibia in a walking mara were calculated as follows: [2] GRF_{axial} = GRF on hind limb · cos(angle of the tibia with respect to the vertical); GRF_{axial} = 48.32 N · cos0.70 = 37.07 N.

The axial component of muscle force (MF) on the tibia is: [3] MF_{axial} = MF · cos(extensor muscle angle with respect to the tibia) = GRF on the tibia · Moment Arm_{GRF} / Moment $Arm_{extensor\ muscle}$.
Moment Arm_{GRF} = metatarsal length · *sin*(metatarsal angle to vertical) (see Fig. 2)
MF_{axial} = 48.32 N · (112.9 mm · sin(0.69 / 26.7 mm) = 130.24 N.

The net axial force on the tibia is: [4] F_{axial} = GRF_{axial} + MF_{axial} = 167.32 N.

The compression stress (CS) due to axial force is: [5] CS_{axial} = F_{axial} / cross-sectional area of the long bone. CS_{axial} = 167.32 N / 61.51 mm^2 = 2.72 MPa.

The cross-sectional area of the tibia CST was estimated by assuming a hollow ellipse as: CST = $\pi/4$ [(D_{ap} external antero-postero diameter · D_{lm} external latero-medial diameter) - (d_{ap} internal antero-posterior diameter · d_{lm} internal latero-medial diameter)] = 61.51 mm^2, where D_{ap}=10.18 mm; D_{lm}=10.68 mm; d_{ap}=5.49 mm; d_{lm}=5.63 mm.

The perpendicular component of the GRF on the tibia is: [6] GRF_{perp} = GRF on the hindlimb · sin(angle of the tibia to the vertical), GRF_{perp} = 48.32 N · sin0.70 = 31.00 N.

The perpendicular component of muscle force on the tibia is: [7] MF_{perp} = sin(angle of extensor muscle with respect to the bone) · GRF on the hindlimb · Moment Arm_{GRF} / Moment $Arm_{extensor\ muscle}$, MF_{perp} = sin(0) · 48.32 N · (112.91 mm · sin(0.69/26.76 mm) = 0.

Net perpendicular force on the tibia is F_{perp} = GRF_{perp} + MF_{perp} = 31.00 N.   The bending stress (BS) on the tibia mid-shaft due to F_{perp}

Table 1 – Ground reaction force (GRF), bone stress, and safety factors estimated during different gaits performed by the mara *Dolichotis patagonum*.

	lateral walk		gallop		half bound		"pronk"	
Speed (m/s)[*]	1.16		6.1		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

[*] from Chagas et al. (2019).

(e.g. Ozkaya and Nordin, 1999) is: [8] BS = M · 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 N · 32 · (84 mm) $\cdot D_{ap}/\pi(D_{ap}^3 \cdot D_{lm} - d_{ap}^3 \cdot d_{lm})$ = 26.14 MPa.

Net tensile stress on the tibia = BS - CS_{axial} = 23.42 MPa. Net compression stress on the tibia = BS + CS_{axial} = 28.86 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; Tab. 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" (Tab. 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 (Tab. 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 mm² (N=4; SD 9.34) whereas for the tibia this value was 61.51 mm² (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 relatively elongated fore and hind limbs, especially due to the lengthening of the tibia and ulna. This condition, which allows performing long strides, is associated with the relatively higher speeds that this species can reach compared to other rodents (Chagas et al., 2019). Elissamburu and Vizcaíno (2004) analyzed morphological characteristics of the limbs focusing on caviomorph rodent species having different locomotion modes, body mass, and habitat. From linear variables measured on fore and hind-limb bones these authors calculated functional indices to assess species morphological adaptations. They found that the tibia robustness index, a

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 (*Protemnodon*)	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
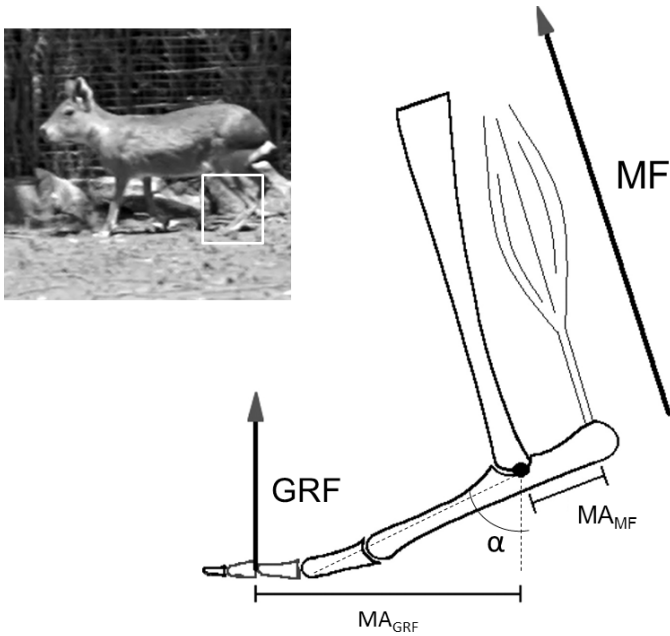
Figure 2 – Estimation of the ground reaction force moment arm (MAGRF) acting on the tibia-metatarsal joint (Biewener, 2003). MA_{GRF} = metatarsal length $\cdot \sin \alpha$ (metatarsal angle to vertical). MA_{MF}: extensor muscle moment arm; GRF: ground reaction force vector; MF: extensor muscle force vector. Insert: walking mara photo captured from a high-speed video.

bone strength indicator calculated as its transverse diameter at mid-shaft divided by its functional length, was not substantially lower in the mara when compared to the values obtained in non cursorial relatively short-limbed species such as *Galea* and *Chinchilla* (Tab. 2 in Elissamburu and Vizcaíno, 2004). This suggests that although maras' hind limbs are proportionally longer than in other rodent species, mainly due to its long tibia, it is also true that this bone has experienced an increase in its diameter, which is probably related with the loads it must bear during fast locomotion.

Estimates of GRF when galloping, running and pronking roughly doubled those estimated for walking. Consequently, the net tensile and compressive stresses on the tibia and humerus during fast gaits are also doubled as compared to walking. These stresses are within the same order of magnitude as those estimated by Alexander et al. (1979) for mammalian species having body masses as different as dog, buffalo and kangaroo, when they run or jump. In the buffalo, the dog and the mara tensile and compressive stress values overlap partially, belonging to the same order of magnitude (Tab. 2), yet their body masses differ in one and two orders of magnitude. This fact suggests that the stresses experienced by limb bones during locomotion are rather similar in animals that differ markedly in body mass as previously proposed by Biewener (1990, 1983) and Currey (2006).

Another factor that could affect bending stresses during fast locomotion is body posture, which may vary during the different gaits. If the angle of limb bones with respect to the vertical is greater, the greater is the component of the peak GRF that generates bending moment, i.e. the component perpendicular to the longitudinal bone axis. As showed in Tab. 1, the angle of the tibia, as well as that of the humerus, were greater when galloping and running as compared to walking, which partly explains the greater bending stress estimated during fast locomotion in maras. However, the mara adopts a relatively upright posture as compared to the typical crouched body posture of rodents in general (Fig. 3). Thus, while the angle of the humerus with respect to the vertical in a galloping mara is 46.5° (Tab. 1), this angle is 56° in the humerus of the rodent *Cavia* moving with the same gait, as can be estimated from Fig. 2 in Rocha-Barbosa et al. (2005). Both species belong to the family Caviidae, but while mara body mass might exceed 8 kg, that of *Cavia* rarely exceeds 900 g. Having a relatively large body mass, maras's body posture could alleviate scaling effects upon muscle supporting forces and bone stress. Biewener (1989) argues that the up-

right posture adopted by animals with greater body mass, by "aligning" the limb bones with respect to the peak GRF, allows reducing both the force that the muscles must exert to support the animal as well as the compressive stress that the limb bones must resist.

The safety factor helps characterize the relationship between the maximum stress (i.e., force per unit area) that the bone is able to endure and the stresses that are confronted by the organism during real performance in nature. The range of safety factor, 3–5.3 during the fastest gaits (Tab. 1), was similar to that found in other mammalian species, of similar or even greater body mass (Biewener, 1982; Alexander, 1981). Safety factors calculated for the tibia were in general lower than those in the humerus which agrees with the greater stress experienced by the hind limb bone. It has been suggested that the stress experienced by limb bones, and their corresponding safety factors, are determinant of the athletic ability (e.g., maximum running speed, maneuverability at fast gaits, coordination) of terrestrial vertebrates, which is relevant when assessing predator-prey relationships (Sorkin, 2008).

It has been proposed that there is an evolutionary parallelism in long bones morphology and locomotion between some cursorial rodent species such as *Cuniculus paca*, *Dasyprocta leporina* and *Myoprocta acouchy* and small sized artiodactyl species such as *Tragulus javanicus* (Rocha-Barbosa et al., 2015; Rocha-Barbosa and Casinos, 2011). When analyzing several parameters that define the biomechanical performance of limb bones such as their cross-sectional area, second moment of inertia, and other indicators of athletic ability these authors found no significant differences between a sample constituted by several species of cavioid rodents as compared to species of artiodactyls. Is the stress experienced by the limb bones of cursorial rodents and artiodactyls similar? For a 70 kg antelope galloping at maximum speed

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

Alexander (1977) estimated bending stresses on the humerus and tibia of 140 and 150 MPa, respectively. In the present study on mara, during the fastest locomotion ("half bounding"), these stresses were estimated at 57.2 and 54.5 MPa for the humerus and tibia, respectively (Tab. 1), less than half of the antelope's values. Since both studies used the same procedure to estimate bone stress, based upon kinematic data, skeletal dimensions and similar assumptions, these differences could be due to the lower duty factors measured in the antelope (0.18–0.20) compared to that of maras (0.33; Tab. 1), most likely due to 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. Caviomorph 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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