On the scaling of mammalian long bones

Guilherme J. M. Garcia and Jafferson K. L. da Silva*

Departamento de Física, Instituto de Ciências Exatas, Universidade Federal de Minas Gerais, Caixa Postal 702, CEP 30123-970, Belo Horizonte – MG, Brazil

*Author for correspondence (e-mail: jaff@fisica.ufmg.br)

Summary

Although there is much data available on mammalian long-bone allometry, a theory explaining these data is still lacking. We show that bending and axial compression are the relevant loading modes and elucidate why the elastic similarity model failed to explain the experimental data. Our analysis provides scaling relations connecting bone diameter and length to the axial and transverse components of the force, in good agreement with experimental data. The model also accounts for other important features of long-bone allometry.

Key words: bone, allometry, mammals, stress, buckling, locomotion, muscle, force.

Introduction

Mammalian long-bone allometry is commonly discussed in terms of the allometric exponents d and l that relate bone diameter D and length L to body mass M *via* the power laws:

$$D \propto M^d \text{ and } L \propto M^l , \qquad (1)$$

where M varies over 6 orders of magnitude. McMahon's proposal, known as the 'elastic similarity model' (ESM), that Euler buckling is the constraint determining the scaling of long-bone geometry, as well as other structural and physiological variables (McMahon, 1973, 1975a), has set the direction of much subsequent work. Although some experimental support was found in ungulates and antelopes (McMahon, 1975b; Alexander, 1977), the predicted exponents are not in agreement with larger data sets embracing a broader range of masses (Alexander et al., 1979b; Biewener, 1983a; Christiansen, 1999a,b; Polk et al., 2000). While the limitation of the elastic similarity model is well documented (Alexander et al., 1979b; Biewener, 1983a; Economos, 1983; Castiella and Casinos, 1990; Christiansen, 1999a,b; Currey, 2002), the physical grounds for this remain unknown.

Mammals adopt several strategies to avoid the mechanical consequences of large size. Biewener (1989, 1990, 1991) has shown that large mammals keep bone stress constant through (i) a shift to a more upright locomotor limb posture and (ii) an allometric increase in the moment arm of antigravity muscles. Those artifices decrease joint moments relative to the magnitude of ground forces, thus reducing mass-specific forces acting on bones. It has also been realized that large mammals do not possess the same locomotor agility of smaller ones, which is probably associated with reduced bone loading and the maintenance of similar safety factors (Biewener, 1991; Christiansen, 1999a,b).

Nevertheless, buckling can suddenly occur even if stress levels are kept at a safe margin. Euler buckling is an elastic instability that occurs when the axial force acting in a rod overcomes a certain threshold. In this paper we show that mammalian long bones are not slender enough to buckle, and that long-bone allometry is governed by the need to resist bending and compressive stresses. We propose a model, based on the requirement to maintain safety factors to yield, which predicts scaling exponents in agreement with data and elucidates various aspects of long-bone allometry, such as differential allometry. Our work, in addition to papers by West et al. (1997, 1999), shows that allometric laws in biology can be understood on the basis of the interplay between geometric and physical constraints.

Note that, although the ESM was formalized in terms of end-loaded columns that may fail in Euler buckling, McMahon (1975a) derived the same scaling relations for a beam subject to pure bending. He considered a rod supported on its extremities and subject to bending by a force proportional to its weight, and showed that if different-sized columns maintain $L \propto D^{2/3}$, the deflection at the center δ divided by the length L is kept constant (McMahon, 1975a). In this sense, the ESM holds that elastic deflections of long bones are self similar across different sizes. This second derivation of the elastic similarity scaling, however, is not consistent with the experimental observation that maximum stresses in mammalian long bones are body-mass-independent (Biewener, 1989, 1990, 1991), since the beam described above will be submitted to stresses proportional to $L^{1/2}$, if δ/L is kept constant. As Currey (2002) states, '*McMahon's basic idea was that organisms are designed so that the deflections they undergo are what is controlled, not the stresses they bear*'. Since this derivation of the ESM is not in agreement with experiment, the hypothesis that remains to be tested is the possibility of Euler buckling.

Currey (2002) investigated this possibility. His analysis indicates that certain long bones are liable to buckling if highly loaded in compression. However, Currey considered solely axial compression, not taking into account that mammalian long bones are subject to a high degree of bending (Biewener, 1991; Rubin and Lanyon, 1982, 1984). As mentioned above, we show that, under axial compression plus bending, mammalian long bones are not slender enough to be vulnerable to Euler buckling.

It is important to observe that, besides Euler buckling, a cylindrical beam, such as a long bone, may also fail due to local buckling. This is characterized by deformation of a small part rather than the deformation of the whole structure, which is what happens in Euler buckling. It occurs when the walls are so thin relative to the diameter that the shape of the structure does not support the wall sufficiently to prevent it from bending in an easy direction (see Currey, 2002). Currey and Alexander (1985) investigated the possibility that mammalian and avian long bones failed in local buckling. They found that the ratio R/t of midradius of the wall (R) to thickness (t) in mammalian long bones is on average 2.0, which is far below the threshold ($R/t=14$) above which long bones would be liable to local buckling.

The balance of this paper is organized as follows. In the next section we provide the mathematical expressions which will be used in our stress analysis. The hypotheses of our model are then presented (The model). In Results and Discussion, we explore the consequences of those hypotheses and compare our predictions with reported experimental values. Finally, we draw our conclusions in the last section.

Theory

In the project of a structure, engineers must know the physical properties of the constituent materials and the forces which each part will endure. This enables the calculation of the dimensions necessary to resist the applied stresses. *In vivo* stresses in bone cannot exceed yield stresses, since this leads to irreversible deformations. Indeed, several investigators (Biewener, 1989, 1990, 1991; Lanyon et al., 1979; Biewener and Taylor, 1986) have shown that maximum stresses *in vivo* maintain a safety factor to yield of about three to four.

The compressive stress σ_c acting on a beam under pure axial compression is:

$$\sigma_c = \frac{F_{ax}}{A} , \qquad (2)$$

where A is the cross-sectional area and F_{ax} is the axial force. On the other hand, a transverse force F_t produces a bending stress σ_b given by:

$$\sigma_c = \frac{F_t\, ry}{I} , \qquad (3)$$

where r is the moment arm of the force, y is the distance from the neutral plane of bending to the specified point and I is the second moment of area. For a hollow cylinder of inner

diameter $d_{inner}=KD$, where $0<K<1$, $A=(1-K^2)\pi D^2/4$ and $I=(1-K^4)\pi D^4/64$ (Gere and Timoshenko, 2000).

A different failure mechanism that must also be avoided is the elastic instability known as Euler buckling. This occurs when the axial force applied to a pillar overcomes a certain threshold. For a biarticulated beam, this threshold is given by the Euler estimate (Gere and Timoshenko, 2000)

$$F_{buckling} = \frac{\pi^2 EI}{L^2} , \qquad (4)$$

where E is the elasticity modulus of the material. In Results and Discussion, we perform some calculations in order to determine which of these failure modes is relevant to long-bone allometry.

The model

Our argument begins along the lines proposed by McMahon (1973, 1975a), namely: (a) a long bone can be described as a cylinder of length L and diameter D; (b) long-bone allometry is determined by the elastic forces the bone must bear; (c) mechanical properties such as elasticity modulus (E) and tension- and compression-yield stresses ($\sigma_{tens\ yield}$ and $\sigma_{comp\ yield}$) are body-mass-independent. Rather than focusing solely on elastic instability (buckling), our model is based on the further hypotheses: (d) although the loading pattern of a long bone is complex, there are only two modes relevant to mammalian long-bone allometry: compression stress σ_c and bending stress σ_b, caused, respectively, by an axial force F_{ax} and a transverse force F_t (see Fig. 1); (e) maximum tensile and compressive stresses *in vivo*, which normally occur in bone's midshaft during locomotion at top velocity, jumping, acceleration and other strenuous activities, maintain a safety factor (S_f) to yield stresses that are body-mass-independent. Euler buckling is avoided by the same safety factor; (f) the ratio $K=d_{inner}/D$ is also body-mass-independent.

Our hypotheses are all supported by experimental data. Assumption (c) agrees with measurements suggesting that bone material properties are size-independent (Biewener, 1982, 1991). Hypothesis (d) is supported by *in vivo* measurements, which show that, in most cases, bending is the main loading mode of long bones and that the principal stresses are almost parallel to the bone longitudinal axis (Biewener, 1991; Rubin and Lanyon, 1982, 1984). Assumption (e) is corroborated by the experimental observation that maximum tensile and compressive stresses measured *in vivo* are approximately 1/3 the bone tensile- and compressive-yield stresses and occur in the midshaft (Biewener, 1989, 1990, 1991; Lanyon et al., 1979; Biewener and Taylor, 1986). Hypothesis (f) is confirmed in various experimental reports. Currey and Alexander (1985) have made a large compilation of values of K for mammals. Analysing these data, we find that K does not correlate with body mass and that its average value is 0.57 ± 0.08. Moreover, if K is a constant, we expect to find $A\propto D^2$ and $I\propto A^2\propto D^4$. Indeed, using the data of Selker and Carter (1989), we find that $A\propto D^{1.98}$ and $I\propto A^{1.98}$. In addition,

Biewener (1982) reports that $I \propto A^{1.99}$. (These scaling relations for A and I were calculated by least squares regression. If reduced major axis (rma) analysis were used, no significant differences would have arisen since the correlation coefficients were always above 0.98.)

Results and Discussion

Euler buckling vs. yield stresses: which is the failure mechanism of mammalian long bones?

We consider a cylindrical beam loaded as in Fig. 1. The beam can fail in two different ways: it will be permanently deformed as soon as yield stresses are reached, and, if the beam is gracile enough, it will buckle before the yield limit. The critical ratio $(L/D)_{cr}$ separating these failure regimes can be estimated as follows. Adopting the convention that tensile stresses are positive and compressive stresses negative, the total stress at point A (Fig. 1) is given by $\sigma_A = -\sigma_c - \sigma_b$, where σ_c is given in Equation 2 and $\sigma_b \propto F_t L D / I$ as given in Equation 3. Similarly, the total stress at point B is $\sigma_B = -\sigma_c + \sigma_b$. We consider here only the maximum values of the stresses developed in long bones, so that our assumption (e) implies that, at maximum loading, $\sigma_A = \sigma_{comp\ yield}/S_f$ and $\sigma_B = \sigma_{tens\ yield}/S_f$. Defining $c = \sigma_{tens\ yield}/\sigma_{comp\ yield}$, it follows (note that $\sigma_{comp\ yield}$ and c are negative with these definitions) that:

$$\sigma_B = c\sigma_A , \qquad (5)$$

$$\sigma_b = \frac{1-c}{1+c}\sigma_c \qquad (6)$$

and

$$\sigma_A = -\frac{2\sigma_c}{1+c} = -\frac{2\sigma_b}{1-c} . \qquad (7)$$

Using the experimental value $c=(128\pm11\ \text{MPa})/(-180\pm13\ \text{MPa})=-0.71\pm0.11$ (Currey, 2002), this result implies that the bending component (σ_b) accounts for approximately $(1-c)/2=86\pm6\%$ of the maximum compressive stress (σ_A) on the bone. To show this, note that $|\sigma_b/\sigma_A|=(1-c)/2=0.855\pm0.055$, while $|\sigma_c/\sigma_A|=(1+c)/2=0.145\pm0.055$. This prediction is in excellent agreement with rosette strain gauge data for tibia, which show that σ_b represents 84.4% of the total stress in dogs and 83.5% in horses during locomotion (Rubin and Lanyon, 1982), and with the values for buffalo (81%) and elephant (89%) obtained through analyses of films of galloping animals (Alexander et al., 1979a).

The maximum axial force F_{ax}^{max} is found substituting $\sigma_c = F_{ax}^{max}/A$ in Equation 7, which provides $F_{ax}^{max} = (1+c)|\sigma_A|A/2$. Since $\sigma_A = \sigma_{comp\ yield}/S_f$, the maximum axial force acting in bone is given by:

$$F_{ax}^{(max)} = \frac{1}{2}(1+c)A\frac{|\sigma_{comp\ yield}|}{S_f} . \qquad (8)$$

In hypothesis (e), we assume that damage due to buckling is prevented by the same safety factor. Thus, the maximum axial force acceptable is:
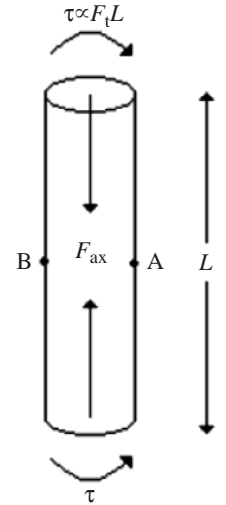

Fig. 1. Bone is described as cylinder loaded with an axial force F_{ax} and a bending moment $\tau \propto F_t L$ acting on its midshaft. For an explanation of points A and B, see text.

$$F_{buckling}^{(max)} = \frac{F_{buckling}}{S_f} = \frac{\pi^2 E I}{S_f L^2} . \qquad (9)$$

We define the dimensionless parameter f as:

$$f = \frac{F_{ax}^{(max)}}{F_{buckling}^{(max)}} , \qquad (10)$$

i.e. the ratio of the axial component of force when yield stress are reached to the axial force that causes buckling. For $f<1$, we have $F_{ax}^{max}<F_{buckling}^{max}$, so that yield stresses are reached before buckling occurs and bone fails due to undesirable permanent deformations. On the other hand, if $f>1$, bone buckles before the yield limit. Therefore $f=1$ is the boundary that separates these two failure regimes.

We will now determine if mammalian long bones are in the region $f<1$, where yield stress is the primary concern, or in the interval $f>1$, for which buckling is the real threat. Substituting Equations 8 and 9 in 10, we find:

$$f = \frac{1}{2}\frac{(1+c)}{\pi^2 E}|\sigma_{comp\ yield}|\left(\frac{AL^2}{I}\right). \qquad (11)$$

The experimental values of the above parameters are $E=22\pm5$ GPa, $\sigma_{comp\ yield}=-180\pm13$ MPa, $c=-0.71\pm0.11$ (Currey, 2002). Thus we find that Euler buckling is avoided provided that $I/AL^2>1.2\times10^{-4}$. Unfortunately experimental reports are usually limited to bone length L and diameter D, and seldom provide cross-sectional area A and second moment of area I. Exceptionally, Selker and Carter (1989) list A, I and L for 40 long bones of 12 species of artiodactyls. In their data, there is no bone in the buckling regime, and the minimum value of I/AL^2 is 3.3×10^{-4}, which is 2.75 times larger than the boundary value. It is worth noting that Biewener (1982) also reports direct measurements of A and I. Nevertheless, since L is not given in this study, Equation 11 could not be used to determine if those bones are liable to Euler buckling.

We have seen in the Theory section that, for a hollow

cylinder of inner diameter $d_{inner}=KD$, we have $A=(1-K^2)\pi D^2/4$ and $I=(1-K^4)\pi D^4/64$. Substituting these values in Equation 11, we find that the 'critical' L/D ratio is:

$$\left(\frac{L}{D}\right)_{cr} = \left(\frac{1}{8(1+c)}\frac{\pi^2 E}{|\sigma_{comp\ yield}|}(1+K^2)\right)^{\frac{1}{2}}, \qquad (12)$$

which corresponds to $f=1$. Substituting the experimental result $K=0.57\pm0.08$ and the mechanical properties of bone related in the previous paragraph, we find that

$$(L/D)_{cr} = 26 \pm 8 \ . \qquad (13)$$

We can now understand why the elastic similarity model fails to explain the experimental data. We have analyzed a large amount of data available in the literature (Alexander et al., 1979b; Biewener, 1983a; Bertram and Biewener, 1992; Christiansen, 1999b) and found that long bones seldom have $L/D>26$. Femura, humerii and tibiae are never more slender than $L/D=26$. Only two of a total of 117 radii are more slender than $(L/D)_{cr}$. On the other hand, ulnae and fibulae are found to exceed this limit often (27 in a group of 68 ulnae examined, and 35 fibulae in a total of 47 exceeded $L/D=26$). This, however, does not necessarily imply that Euler buckling determines the allometry of those bones; it probably simply reflects their non-load-bearing condition in some animals (Christiansen, 1999a,b).

It is important to note that the uncertainty in the value of $(L/D)_{cr}$ is quite large as a consequence of the variation observed experimentally in the physical (E, $\sigma_{tens\ yield}$ and $\sigma_{comp\ yield}$) and geometrical (K) properties of bone. Nevertheless, the discussion above is still correct even if we choose the smallest estimate for $(L/D)_{cr}$, namely, $(L/D)_{cr}=18$.

Determining the scaling exponents d and l

Let us derive the allometric exponents d and l defined in Equation 1. As shown in Fig. 1, we describe the resultant force acting on half-bone by two components, namely an axial component F_{ax} and a transverse component F_t. There is no *a priori* reason to assume that, at maximum loading, the components F_{ax}^{max} and F_t^{max} are proportional to each other. Therefore, we consider that each component scales with its own allometric exponent, i.e. $F_{ax}^{max}\propto M^{a_x}$ and $F_t^{max}\propto M^{a_t}$. Below, we show that generally $a_x\neq a_t$. The exponents a_x and a_t will be deduced from experimental data on the scaling of muscle force, ground reaction force and direct measurements of the forces acting on a long bone.

We now show how the scale-invariance of bone mechanical properties, safety factor and ratio K lead to the power-law dependence of bone dimensions on body mass (Equation 1). For $f<1$, the bone fails when the maximum stresses reach the yield limit. Since yield stresses and safety factors are body-mass-independent [assumptions (c) and (e)], equation 8 implies that $F_{ax}^{max}\propto A$. Substituting $A\propto D^2\propto M^{2d}$, we find the scaling relation $2d=a_x$ [here we have used assumption (f)].

Equation 3 implies that the maximum transverse force acting on a bone is $F_t^{(max)}\propto\sigma_b^{(max)}I/DL$. From Equation 7 we have that the maximum bending stress $\sigma_b^{(max)}$ in bone is $\sigma_b^{(max)}=(1-c)\sigma_{comp\ yield}/2S_f$, which is body-mass-independent. Consequently $F_t^{(max)}\propto I/DL\propto M^{3d-1}$ and, since $F_t^{(max)}\propto M^{a_t}$, we have our second scaling relation, which is $3d-l=a_t$. Therefore the scaling exponents for non-gracile bones are:

$$d=\frac{a_x}{2} \quad \text{and} \quad l=\frac{3a_x}{2}-a_t. \qquad (14)$$

In order to estimate d and l, we use the experimental values of a_x and a_t. Although McMahon assumed that $F_{buckling}=F_{ax}\propto M$ ($a_x=1$) (McMahon, 1973, 1975a), the loading situation of a long bone is not so simple. The usual procedure (Alexander, 1974; Alexander et al., 1979a; Biewener, 1983b) to evaluate the forces acting on bones using force platform recordings is to equate the moments exerted by muscle force (F_{muscle}) and ground reaction force (F_{ground}): $F_{muscle}r=F_{ground}R$, where r and R are the moment arms defined in Fig. 2. The forces exerted in a bone can then be written as $F_{ax}=F_{muscle}\cos(\alpha_m)+F_{ground}\cos(\alpha_g)$ and $F_t=-F_{muscle}\sin(\alpha_m)+F_{ground}\sin(\alpha_g)$, where α_m and α_g are measured with respect to the bone longitudinal axis. Since muscle forces are almost parallel to the bone axis ($\alpha_m\leqslant10°$) and $F_{muscle}\gg F_{ground}\cos(\alpha_g)$, because $\cos(\alpha_g)<1$ and, in general, $r<R$, we assume $F_{ax}\propto F_{muscle}$ and $F_t\propto F_{ground}\sin(\alpha_g)$.

The scaling of F_{ax} is determined in three different ways. First, it appears that maximum muscle stress is approximately independent of body mass (Schmidt-Nielsen, 1990), which implies that muscle force is proportional to muscle area, so that $F_{muscle}\propto A_{muscle}\propto M^a$. We have collected and calculated averages of muscle-area allometric exponents from several sources. The results are as follows: $a=0.77$ for antelopes (Alexander, 1977), $a=0.83$ for insectivores and rodents (Castiella and Casinos, 1990), $a=0.78$ for rodents (Druzinsky,
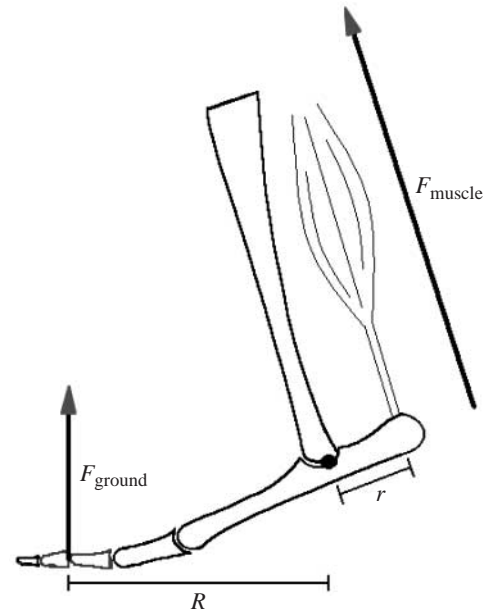

Fig. 2. A simplified loading situation. R is the moment arm of the ground force (F_{ground}), while r is the moment arm of the muscle force (F_{muscle}). Figure modified from Biewener (1989).

Table 1. *Bone length and diameter scaling exponents* l *and* d *for the main long-bones*

Bone	Scaling exponents					
	l_{lsr}/l_{rma}	d_{lsr}/d_{rma}	$2d$	$3d-l$	r_l	r_d
All mammals						
Femur	0.301/0.309	0.355/0.360	0.710/0.720	0.764/0.771	0.976	0.986
Tibia	0.257/0.277	0.360/0.365	0.720/0.730	0.823/0.818	0.929	0.985
Fibula	0.225/0.243	0.338/0.368	0.676/0.736	0.789/0.861	0.926	0.918
Humerus	0.300/0.311	0.382/0.386	0.764/0.772	0.846/0.847	0.964	0.989
Radius	0.300/0.321	0.387/0.401	0.774/0.802	0.861/0.882	0.933	0.964
Ulna	0.302/0.318	0.355/0.458	0.710/0.916	0.763/1.056	0.949	0.776
Average 1	0.281/0.297	0.363/0.390	0.726/0.779	0.808/0.873	–	–
Average 2	0.290/0.305	0.371/0.378	0.742/0.756	0.824/0.830	–	–
Non-gracile mammals only						
Fibula	0.235/0.241	0.279/0.286	0.558/0.572	0.602/0.617	0.979	0.978
Ulna	0.288/0.298	0.376/0.383	0.752/0.766	0.840/0.851	0.966	0.980

Average 1, mean for all the 6 bones; average 2, mean for femur, tibia, humerus and radius.

Below are the values of the exponents for non-gracile ($L/D<26$) ulnae and fibulae.

The data were taken from Christiansen (1999b).

The exponents are given for both methods: least square regression (lsr) and reduced major axis (rma). r_l and r_d are the correlation coefficients. For further explanation, see text.

1993) and $a=0.80$ and 0.81 for mammals as a whole (Alexander et al., 1981; Pollock and Shadwick, 1994). We note that mammals of very different body masses, such as rodents and antelopes, exhibit similar behavior, with muscle area scaling on average as $M^{0.80}$ (individual muscle exponents range from 0.65 to 0.92). Second, measuring the effective mechanical advantage ($EMA=r/R\propto M^{0.26}$) and using his previous result that $F_{ground}\propto M$ in small mammals, Biewener (1989) reported that $F_{muscle}\propto M^{0.74}$ and predicted maximum muscle stress to scale as $M^{-0.06}$, a prediction that has yet to be confirmed. (Note that this result is consistent with the scaling of muscle force and area mentioned above). Third, the only direct estimate of a_x that we are aware of was given by Rubin and Lanyon (1984) and, although based in a small sample (5 species), provides a value ($a_x=0.69$) consistent with the scaling of muscle force. These results allow us to predict:

$$d \approx 0.37 \ , \tag{15}$$

since $a_x \approx 0.74$. This is in good agreement with experimental values, as shown in Tables 1 and 2. Notice that even if we choose the highest ($a_x \approx 0.80$) or the lowest ($a_x \approx 0.69$) estimates for the allometric exponent of axial force, the predicted value for d, namely $0.69 \leqslant 2d \leqslant 0.80$, is still in the experimental range.

The experimental exponents presented in Table 1 were taken or calculated from Christiansen (1999b). We chose these data for two reasons: (i) they represent the most extensive sample, and (ii) animals with similar locomotor modes are included. (Note that Christiansen's data has an inconvenience, namely, animals of mass <1 kg are not included.) The agreement of the predicted value of d with the experimental exponents reinforces that long-bone allometry is governed by the need to resist compressive and bending stresses. Notice that the

correlation coefficients are much higher when we consider only non-gracile ulnae and fibulae.

In contrast to the assumption of McMahon (1973, 1975a) that bone mass is proportional to body mass ($D^2L\propto M$), Christiansen (2002) has recently shown that bone mass scales with slight positive allometry (on average, bone mass scales as $M^{1.06}$ using the rma method). Indeed, the assumption $D^2L\propto M$ together with our result $d\approx 0.37$ leads to a poor prediction of the bone length exponent ($l\approx 0.26$) in comparison to the experimental value ($l\approx 0.30$) (Table 1). Therefore the positive scaling of long-bone mass, although weak, cannot be ignored. This point has already been noted by Hokkanen (1986).

Here we make a digression regarding the pioneering work of Prange and collaborators (1979) on the scaling of mammalian skeletal mass ($M_{skeletal}$). Since their work was published, it has been widely cited as evidence that mammalian skeletal mass scales with positive allometry (for instance, see Schmidt-Nielsen, 1984). Their data, however, is not entirely conclusive. Among the 49 mammals used in the study, only the elephant has a body mass above 70 kg. Moreover, it seems that man and dog have skeletal masses above the values expected for their body masses. Fitting their data for the 44 mammals with masses less than 12 kg using the least-square regression method, we find $M_{skeletal}=0.061M^{1.02}$, $r=0.993$. (Note that rma analysis would not change this result appreciably due to the high correlation coefficient.) In agreement with this result, Bou and Casinos (1985) found that $M_{skeletal}=0.04225M^{1.0143}$, $r=0.993$, in insectivores and rodents. Therefore, experimental data indicates that skeletal mass is proportional to body mass for mammals smaller than 12 kg. It is necessary to collect more data in the gap between 67 kg (man) and 6600 kg (elephant) in order to obtain a more reliable equation for the whole group of mammals. Finally, we note

Table 2. *Experimental values of* l *and* d *for non-gracile long bones (L/D<26) using data obtained from various sources*

Bone	Alexander		Bertram and Biewener		Christiansen	
	l_{lsr}/l_{rma}	d_{lsr}/d_{rma}	l_{lsr}/l_{rma}	d_{lsr}/d_{rma}	l_{lsr}/l_{rma}	d_{lsr}/d_{rma}
Small mammals (M<50 kg)						
Femur	0.398/0.404	0.369/0.371	0.372/0.384	0.380/0.392	0.327/0.342	0.344/0.362
Tibia	0.344/0.350	0.379/0.383	0.362/0.376	0.388/0.403	0.343/0.364	0.373/0.387
Humerus	0.393/0.399	0.382/0.384	0.382/0.395	0.391/0.405	0.321/0.351	0.386/0.401
Radius	–	–	0.397/0.419	0.394/0.414	0.364/0.407	0.453/0.481
Ulna	0.383/0.389	–	–	–	0.288/0.336	0.371/0.406
Average 2	0.378/0.384	0.377/0.379	0.378/0.394	0.388/0.404	0.339/0.366	0.389/0.408
Large mammals (M>50 kg)						
Femur	0.325/0.385	0.315/0.329	0.284/0.326	0.308/0.344	0.280/0.310	0.354/0.367
Tibia	0.198/0.248	0.304/0.334	0.142/0.207	0.315/0.358	0.203/0.279	0.338/0.356
Humerus	0.323/0.371	0.365/0.381	0.286/0.327	0.320/0.358	0.288/0.323	0.359/0.370
Radius	–	–	0.225/0.297	0.430/0.473	0.275/0.346	0.311/0.362
Ulna	0.282/0.319	–	–	–	0.255/0.290	0.405/0.431
Average 2	0.282/0.335	0.328/0.348	0.234/0.289	0.343/0.383	0.262/0.311	0.341/0.364

Data was taken from Alexander et al. (1979b), Biewener (1983a), Bertram and Biewener (1992) and Christiansen (1999a,b).

Mammals are considered small or large relative to M=50 kg, as proposed by Christiansen (1999b).

Average 2 is the mean defined in Table 1.

that different bones scale with different allometric exponents. While long-bone masses scale with significant positive allometry (Bou and Casinos, 1985; Christiansen, 2002), the masses of other bones, such as the skull, scale with significant negative allometry (Bou and Casinos, 1985).

It was relatively easy to estimate a_x. By contrast, the exponent a_t is more difficult to evaluate because it depends on the scaling of ground reaction force (F_{ground}) and experimental reports for this are scarce. As stated above (The model), maximum stresses may occur in different activities, such as galloping at top speed, jumping and acceleration. Here we evaluate the exponent a_t only during top speed locomotion, since we did not find any experimental data for the scaling of F_{ground} in jumping nor in accelerating. Nevertheless, this does not seem to be a shortcoming, since maximum tensile stresses during top speed locomotion maintain the same safety factor to yield that are kept by compressive stresses (Biewener, 1989, 1990, 1991; Lanyon et al., 1979; Biewener and Taylor, 1986). This means that, although the magnitude of ground reaction forces may be larger during acceleration or jumping in comparison to top speed locomotion, the allometric exponent a_t is probably the same for these three vigorous activities.

Large ground reaction forces occur during top speed locomotion and are known to scale as M/β, where β is the duty factor (fraction of the stride during which a foot touches the ground). Alexander et al. (1977) reported that in ungulates, $\beta \propto M^{-0.11}$ (r_β=0.79) for the fore feet and $\beta \propto M^{-0.14}$ (r_β=0.78) for the hind feet. When analyzing allometric data, the least-square regression (lsr) method is not expected to be the most appropriate, since it assumes that error is present only in the dependent variable. Reduced major axis (rma) analysis is to be preferred because it takes the uncertainties of both variables

into account (Christiansen, 1999a,b; Sokal, 1981). Reanalysing Alexander's data using rma, we obtain the exponents −0.14 and −0.18, for fore and hind feet, respectively. Since there is no apparent posture change in large mammals (Biewener, 1989, 1990), we assume that the angle α_g is constant; then $a_t \approx 0.84$ for these animals. This estimate implies that $l=3d-a_t \approx 0.27$ in large mammals, in reasonable agreement with the experimental data (see Table 2). On the other hand, small mammals change posture from a crouched to a more upright position (Biewener, 1989, 1990), and consequently the angle α_g diminishes with increasing body mass ($\alpha_g \propto M^{-0.07}$ in small mammals at the trot–gallop transition speed; Biewener, 1983a). As already mentioned, Biewener reported that $F_{ground} \propto M^{1.0}$ in this group at top galloping speed. Thus, considering that α_g scales at top velocity in the same manner as at the trot–gallop transition speed, one predicts that $a_t \approx 0.93$ in small mammals. This result, however, does not agree with the experimental data. The calculation of a_t for small mammals needs further study, as discussed below.

Selker and Carter (1989) found that $a_t=3d-l \approx 0.80$ using their data for bone dimensions of artiodactyla, and Biewener's of mammals. Knowing that muscle force scales approximately as $M^{0.80}$, they concluded that the transverse component of force is proportional to muscle force ($F_t \propto F_{muscle}$). However, this conclusion is in contrast with the widely accepted analysis (Alexander, 1974; Alexander et al., 1979a; Biewener, 1983b) of the loading situation in legs, which led us to the conclusion that the transverse component of force (F_t) is proportional to ground reaction force, not muscle force. Moreover, if we accept $F_t \propto F_{muscle}$, we would conclude that $a_x=a_t$ and so $l=d \approx 0.37$. Although this is a reasonable result for small mammals (see Table 2), large mammals do not follow this relation. In order to

solve this puzzle, more data are needed on the scaling of maximum muscle stress, bone mechanical properties and duty factor to confirm if they are mass-independent or if they exhibit a small, but relevant, variation with size. It is also very important to measure a_t experimentally, as Rubin and Lanyon (1984) did for a_x, and also to improve the measurement of a_x, presently based on strain data for only five species (see discussion above). We recognize that those experiments are difficult, because rosette strain gauges can only be used to record strains from bones of a certain size – very small bones cannot be studied in this way. Nevertheless, the arguments presented here show that, in order to completely describe long-bone allometry, one needs to determine which are the forces applied on bone <u>and</u> their scaling with body mass.

Finally, the model presented here accounts for two further important aspects of bone allometry not explained by McMahon's elastic similarity (McMahon, 1973, 1975a). First, it has been realized that long-bone allometry exhibits different scaling regimes for small and large mammals (Table 2) and that this should be related to a posture change found mainly in small mammals and to the reduced locomotor performance of large mammals (Economos, 1983; Biewener, 1989, 1990; Bertram and Biewener, 1990; Christiansen, 1999a,b). Our model confirms this distinction between regimes by coupling the allometric exponents with ground reaction forces, and angles of force to bone, both of which are body-mass dependent. (Note that this coupling makes it possible to study the forces involved in the locomotion of extinct species, such as dinosaurs, using bone-allometry data.) Second, Christiansen reported that large mammals develop progressively *shorter* limb bones as a means of reducing bending stress, rather than proportionally *thicker* bones (Christiansen, 1999b). This fact is a direct consequence of our analysis. We have shown that $F_{ax} \propto F_{muscle}$ and that muscle–force allometry does not distinguish small and large mammals. Thus Equation 14 implies that d must have similar values for all mammals and, therefore, differential scaling can only appear in differences of l.

Conclusions

In summary, we propose a model that predicts scaling exponents in agreement with experiment, and that also accounts for the other important features of mammalian long-bone allometry. Those results have not been explained by any previous model. In particular, we elucidate why McMahon's elastic similarity model is not obeyed, a long-standing puzzle in this field. Our model sets the direction for the description of avian and reptile long-bone allometry and provides a means to study the problem of terrestrial locomotion of extinct and extant species.

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