

BONE STRENGTH IN SMALL MAMMALS AND BIPEDAL BIRDS: DO SAFETY FACTORS CHANGE WITH BODY SIZE?

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SUMMARY

Measurements of the cross-sectional geometry and length of bones from animals of different sizes suggest that peak locomotory stresses might be as much as nine times greater in the limb bones of a 300 kg horse than those of a 0.10 kg chipmunk. To determine if the bones of larger animals are stronger than those of small animals, the bending strength of whole bone specimens from the limbs of small mammals and bipedal birds was measured and compared with published data for large mammalian cortical bone (horses and bovids). No significant difference ($P > 0.2$) was found in the failure stress of bone over a range in size from 0.05–700 kg (233 ± 53 MN/m² for small animals compared to 200 ± 28 MN/m² for large animals). This finding suggests that either the limb bones of small animals are much stronger than they need to be, or that other aspects of locomotion (e.g. duty factor and limb orientation relative to the direction of the ground force) act to decrease peak locomotory stresses in larger animals.

INTRODUCTION

An important assumption made by allometric studies of vertebrates is that the material strength of bone is the same for both large and small animals (McMahon, 1975*a*; Alexander, 1977; Alexander, Maloij, Hunter, Jayes, & Nturibi, 1979). This assumption has not been tested directly, but it seems reasonable because measurements of the strength of compact bone specimens from large mammals have yielded fairly uniform results (see Currey, 1970, for a review). Moreover, both the histology and the organic and mineral composition of different types of compact bone tissue, such as lamellar, woven and Haversian bone, are generally similar for a variety of vertebrates studied (Enlow & Brown, 1957, 1958; Bourne, 1972).

Scaling arguments suggest, however, that the material strength of bone may vary with body size. Geometric similarity provides the simplest description of how animals change with size. To maintain the same shape, all linear dimensions, such as length (l) and diameter (d), are uniformly proportional to body mass (M_b) to the one-third power and area dimensions are proportional to $M_b^{2/3}$. Galileo (see Thompson, 1915) was probably the first person to observe that if animals are geometrically

scaled replicas of one another, with the same physical proportions and using the same materials, there is a limit to how large structures and animals can be built without failing under their own weight. Discussing the 'principle of similitude', d'Arcy Thompson (1917) later observed that although animals appear to scale in a regular way with size, shape changes are involved, so that large animals appear more robust than small animals. Recent empirical data have shown however that geometric similarity is maintained in the skeletal dimensions of mammals varying over a wide size range. Alexander, Jayes, Maloij & Wathuta (1979) measured the lengths and diameters of the principal limb bones from 37 species of terrestrial mammals, representing seven orders, that ranged in size from a shrew to an elephant. Despite differences in the animals' external shape, the empirical results over the entire size range were in agreement with what would be predicted by geometric similarity ($l \propto M_b^{0.35}$ and $d \propto M_b^{0.36}$). These exponents are slightly greater than the predicted value of 0.33, however, showing that larger animals do tend to have proportionately larger bones. This is consistent with the finding that skeletal mass scales to $M_b^{1.09}$ (Prange, Anderson & Rahn, 1979).

We can use these allometric relationships to predict the stress developed in the limb bones of an animal simply supporting its own weight. In the case where the forces acting on a bone load it in axial compression (see Fig. 1a) the compressive stress (σ_c) acting in the bone's cortices will be:

$$\sigma_c = F_c/A, \quad (1)$$

where F_c is the compressive force acting on the bone and A is its cross-sectional area. In the case where the forces acting on a bone exert a bending moment (force times the length of the moment arm) about the bone's midshaft (see Fig. 1b) the bending stresses (σ_b) developed at the surface of the bone's cortices, based on linearly elastic theory, will be:

$$\sigma_b = \frac{(F_b r) c}{I} \quad (2)$$

where F_b is the bending force, r is the moment arm, c is the distance from the neutral plane of bending to the surface of the bone's cortex, and I is the second moment of area of the bone at its midshaft.

This assumes of course that an animal's skeleton is designed to resist static gravitational forces, which seems unlikely. Because animals presumably are built to move about, dynamic forces must be an important influence on the design of the skeleton as well. McMahon (1977) has argued that the peak force exerted on the ground by an animal's limb is independent of size for animals running at their trot-gallop transition. Accordingly, if we assume that the peak dynamic forces that act on the limb bones of an animal during locomotion are a constant multiple of the force exerted due to gravity acting on the animal's mass ($F_w = M_b g$) and that this proportionality is independent of size, so that F_c and F_b are both proportional to $F_w^{1.0}$, then both equations (1) and (2) still hold.

Because $A \propto d^2 \propto F_w^{0.72}$ (according to the empirical results of Alexander, Jayes *et al.* 1979) equation (1) shows that:

$$\sigma_c \propto F_w^{0.28}. \quad (3)$$

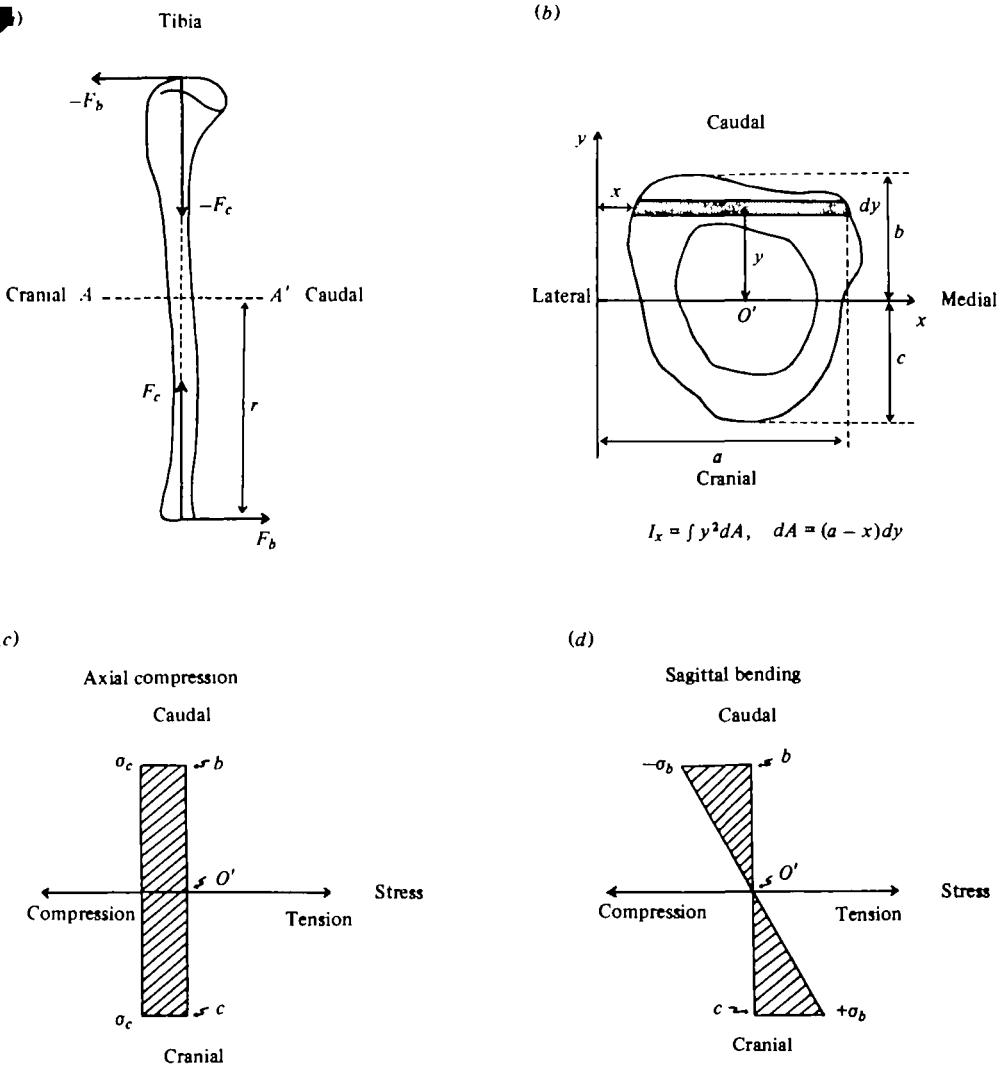


Fig. 1. (a) shows the two principal loading situations discussed in the text, axial compression (F_c) and antero-posterior bending (F_b), acting on a tibia. (b) is a drawing of the cross-section of the tibia at its midshaft ($A-A'$), the point at which the bones were broken, and shows how the second moment of area (I) was computed. (c) and (d) show the stress fields acting across the cortex of the bone at the level of its midshaft for axial compression and sagittal bending, respectively, assuming that cortical bone is homogeneous and linearly elastic.

The corresponding allometric relations for determining the stress due to bending based on Alexander, Jayes *et al.*'s (1979) data are: $r \propto F_{10}^{0.35}$, $c \propto F_{10}^{0.36}$, and $I \propto F_{10}^{1.44}$. Equation (2) can then be reduced to:

$$\sigma_b \propto F_{10}^{0.27}, \tag{4}$$

which is very similar to the result obtained for stresses developed due to compressive forces acting on the bone.

This means that, for example, a 1000-fold increase in body mass will result in a seven-fold increase in the peak compressive stress and a 6.5-fold increase in the peak bending stress acting in the limb bones of the larger animal. If the material strength of bone loaded in compression or bending is constant, this implies that large animals have a smaller safety margin and develop stresses that are much nearer their fracture (or ultimate) strength than do small animals, or that small animals are 'wasteful' of bone tissue and are built to have unreasonably high safety margins.

However, if the material strength of bone increases with increasing size, then a similar margin of safety could be maintained for large and small animals. Although other features of the skeleton's support of dynamic forces may effect the stress that acts in a bone's cortex, such as the orientation of the limb relative to the direction of the ground force exerted at the foot and the fraction of the stride period that a limb is in contact with the ground (defined as the duty factor); a critical study is necessary to ascertain whether there is in fact a significant difference in the material strength of bone between large and small animals.

To test this, the fracture strength was determined for the principal limb bones from a variety of species of small mammals and bipedal birds (body mass from 0.050–0.622 kg), which were loaded in three-point bending and compared with values reported for large mammals. Bending was chosen because of its relative ease and accuracy as a mechanical test of strength, especially for whole bones, and because it has been shown that the limb bones of a variety of animals are most often subjected to bending forces during locomotion; both compressive and torsional loads are typically much smaller (Lanyon & Baggott, 1976; Lanyon & Bourn, 1979; Alexander & Vernon, 1975; and A. A. Biewener, J. Thomason, A. E. Goodship & L. E. Lanyon, in press).

MATERIALS AND METHODS

Specimens of the following species were weighed and killed: three species of rodents which run quadrupedally – rats (*Rattus norvegicus*), chipmunks (*Tamias striatus*), and ground squirrels (*Spermophilus tridecemlineatus*); one species of rodent that hops bipedally – kangaroo rats (*Dipodomys spectabilis*); and two species of bipedal birds – Chinese painted quail (*Excalfatoria chinensis*) and bobwhite (*Colinus virginianus*). The principal limb bones were dissected and placed in physiological saline. Care was taken not to scratch or cut into the cortex of the bones to avoid introducing stress concentrations during testing. The bones were either tested immediately after dissection or frozen in physiological saline at -25°C . Frozen bones were allowed to reach room temperature before being tested. All specimens were tested at 21°C .

The apparatus used to break the bones is shown in Fig. 2. The load was applied at a uniformly increasing rate to the distal end of the bone via a stainless steel wire looped about the distal end of the bone. The bending force was applied by screwing the drive rod through the bar to which the wire was attached. The proximal end of each bone was fixed rigidly in a mold of dental methacrylate. Care was taken to keep the bones moist during the fixation period and during each test. The force was measured by differential output from two metal foil strain gauges attached to the

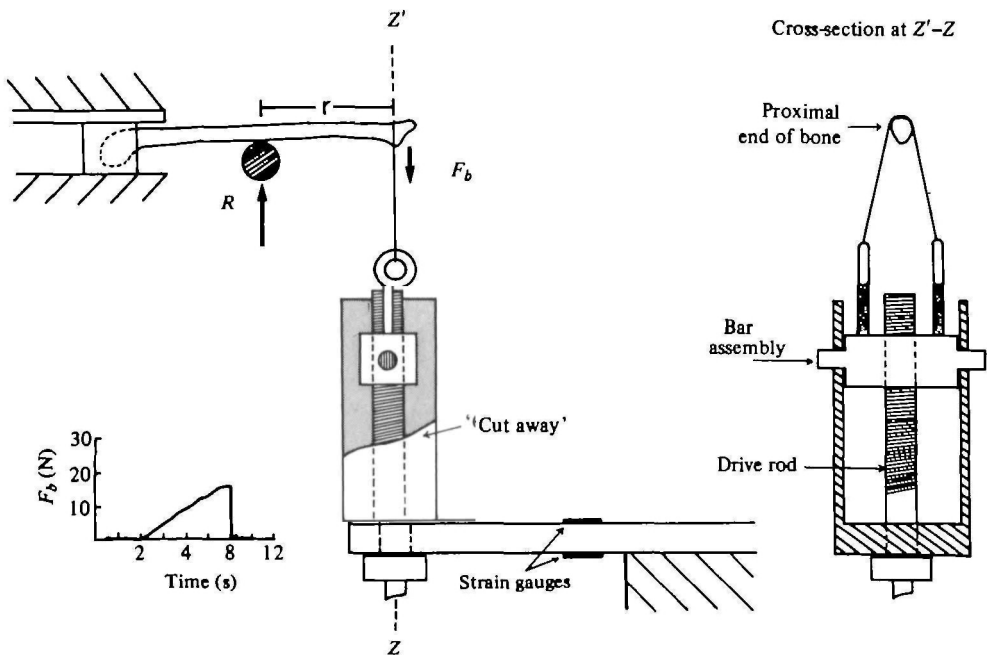


Fig. 2. A schematic drawing of the device used to load the whole bone specimens to failure in three point bending. The applied bending force (F_b), moment arm (r) and the reaction force (R) are shown. The drawing to the right shows an end-on view of the threaded drive rod and its assembly for applying the bending moment to the distal end of the bone, drawn from a cross-section taken at $Z'-Z$. The lower left inset shows a representative record of the force trace for a ground squirrel femur.

steel beam across a Wheatstone bridge circuit using a strain gauge bridge amplifier (model no. 2120, Vishay Instruments, Inc.). The loading device was calibrated with known weights before and after each series of tests was performed. The response of the device was linear over the range of forces applied. Each bone was adjusted so that a steel rod exerted the reaction force at the bone's midshaft; the rod was 9.5 mm in diameter to minimize the error due to local stress concentration. The length of the moment arm was measured from the centre of the rod to the point of application of the bending force.

After each test the broken ends of the bone were embedded in epoxy resin and ground down until a smooth cross-section was attained as close as possible to the site of fracture. The cross-sections were photographed and projected onto a screen with known magnification. Tracings of the cross-sections about the periosteal and endosteal surfaces were then analysed using a digitizing table and PDP-11 microprocessor to determine the cross-sectional area (A), the centroid of the cross-section (O'), the second moment of area (I), and the maximum distance from the neutral plane of bending to the tensile surface of the bone's cortex (c) (see Fig. 1). The means of the two values for c and I from the proximal and distal segments of each bone were used, along with the moment arm (r) and the bending force (F_b), to calculate the ultimate stress of the bone according to equation (2). Using this same procedure, measure-

ments of cross-sectional area and second moment of area were also made of a series of additional bones to determine more accurately how each of these parameters scales to body mass, rather than deriving the allometric relationships based on the data for diameter given by Alexander, Jayes *et al.* (1979). These measurements were made at the midshaft of each bone, where stresses due to bending are likely to be greatest.

GLOSSARY OF SYMBOLS USED IN THE TEXT

l	length;
d	diameter;
A	cross-sectional area;
r	moment arm about a bone's midshaft (equals one-half the bone's length);
c	distance from the neutral axis to the bone's cortex;
I	second moment of area;
O'	centroid of the bone cross-section at its midshaft;
M_b	body mass;
g	acceleration due to gravity;
F_w	force exerted due to the effect of gravity on an animal's body mass;
F_c	compressive force exerted on a bone;
F_b	bending force exerted on a bone;
σ_c	stress due to compression;
σ_b	stress due to bending;
σ_{ult}	fracture stress.

RESULTS

The allometric equations determined from a least squares linear regression analysis of the data for cross-sectional area and second moment of area (for bending in the antero-posterior plane) show that: $A \propto M_b^{0.73}$ and $I \propto M_b^{1.43}$. These measurements were made for a series of bones from eleven species of mammals ranging in size from 0.038–276 kg. The data are presented in Table 1. Graphs of area and second moment of area plotted against body mass on logarithmic co-ordinates are shown in Fig. 3a and b, respectively. The regression lines calculated from the data are drawn in each case. The equation of each line and its coefficient of determination are included as well.

Using these values for the exponents relating cross-sectional area and second moment of area to body mass, the scaling of peak compressive and peak bending stresses to the force exerted due to the effect of gravity on body mass become:

$$\sigma_c \propto F_w^{0.28}, \quad (5)$$

and

$$\sigma_b \propto F_w^{0.28}. \quad (6)$$

The results of the bending tests show that the mean values of the ultimate bending strength of the different limb bones tested within each group were not significantly different ($P > 0.1$). Nor was the mean value of ultimate bending strength significantly

Table 1. Cross-sectional area (A) and second moment of area (I) measured at the mid-shaft of the principal limb bones indicated. Each value presented represents the mean of each bone measured

Animal	Body mass (kg)	Bone	A (mm ²)	I (mm ⁴)	No
Mouse	0.038	Femur	1.63	0.73	4
		Tibia	0.88	0.82	4
		Humerus	0.86	0.072	4
Kangaroo rat	0.103	Femur	3.60	1.54	4
		Tibia	3.84	2.17	4
Ground squirrel	0.117	Femur	2.03	0.96	4
		Tibia	1.34	0.57	4
		Humerus	2.17	0.92	4
Rat	0.522	Femur	5.28	3.11	6
		Tibia	8.42	7.14	6
		Humerus	6.63	9.53	6
Guinea pig	0.630	Femur	9.36	11.10	4
		Tibia	6.12	5.07	4
Cat	3.52	Humerus	5.56	5.60	4
		Femur	33.8	144.2	4
		Tibia	37.5	152.9	4
Colobus monkey	12	Humerus	33.9	119.8	4
		Femur	86.2	817.1	2
		Tibia	70.8	681.7	2
Dog*	20	Humerus	62.0	381.0	2
		Radius	89.0	970	4
		Man†	60	Femur	325.2
Horse	276	Tibia	246.8	16700	120
		Tibia	808	70000	3
		Metatarsus	464	22300	3
		Radius	641	36100	3
		Metacarpus	454	19400	3

* Data from Carter, Harris, Vasu & Caler, 1981.

† Data from C. B. Ruff, personal communication.

different between the two groups: 228 ± 46 MN/m² (\pm S.D.) for the small mammals and 239 ± 69 MN/m² (\pm S.D.) for the small birds ($P > 0.1$). The mean value for the ultimate bending strength of all of the bones tested was 233 ± 53 MN/m² (\pm S.D.). These data are presented in Table 2 for the small mammals and in Table 3 for the small birds. In the case of the rat femora, tibiae and humeri, a series of twelve bones each were broken to assess the reliability of the experimental technique employed. The standard deviation about the mean was less than 14% of the mean for each series of bones. The data for the small mammals and birds can be compared with the values of ultimate bending strength reported for large mammals which are presented in Table 4, along with additional data reported for rat femora and tibiae.

A graph of ultimate bending stress plotted against body mass on logarithmic co-ordinates (Fig. 4) shows that there is no difference in the bending strength of bone over a range in size from 0.05–700 kg. The slope of the regression line for the data is -0.011 ($R^2 = 0.046$) and is not significantly different from zero. The dashed line represents a plot of bending strength *v.* body mass that would be necessary to maintain a uniform safety margin for animals of different size assuming that peak locomotory stress scales to $F_w^{0.28}$, according to the results for cross-sectional area and

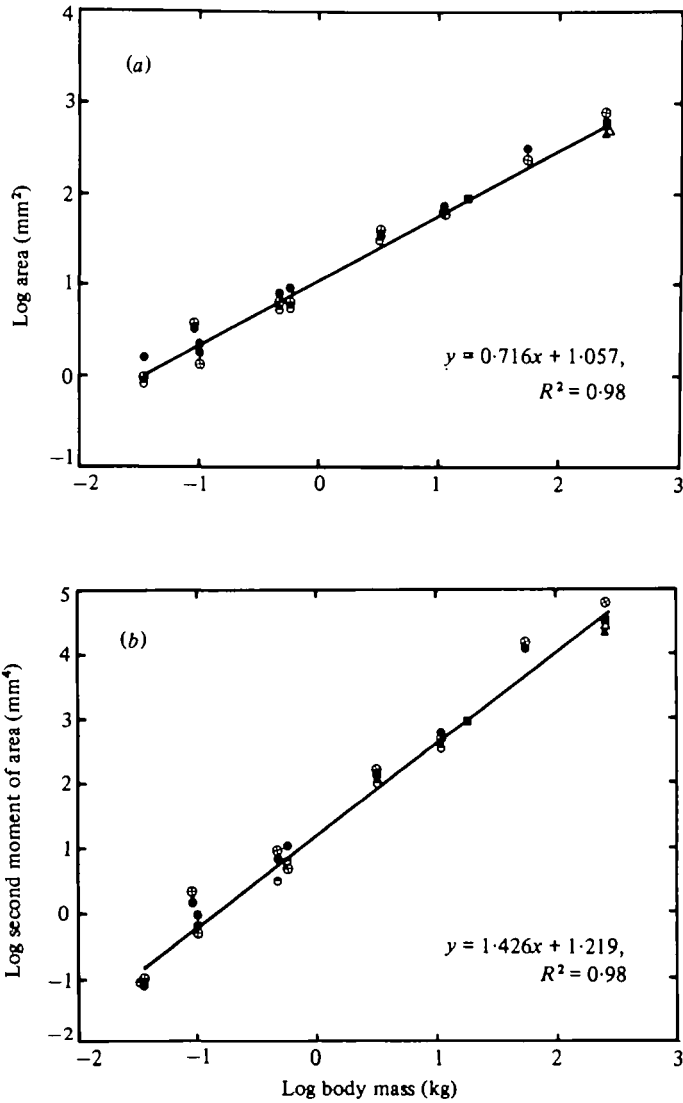


Fig. 3. (a) a graph of bone cross-sectional area (measured at the midshaft) plotted against body mass on logarithmic co-ordinates. (b) a graph of the second moment of area (measured at the bone's midshaft) for bending in the antero-posterior direction plotted against body mass on logarithmic co-ordinates. Each point plotted represents the mean of the values determined for each bone measured from each species. The different bones measured are denoted by their respective symbols (● femur, ⊕ tibia, ⊖ humerus, ■ radius, ▲ metacarpus, and △ metatarsus). A total of 27 values comprising eleven species are shown in each graph. The equation of the line obtained from a least squares linear regression analysis for area *v.* body mass (M_b) is:

$$\log A \approx 0.716 \log M_b + \log 1.06, \quad R^2 = 0.98,$$

and for second moment of area *v.* body mass it is:

$$\log I = 1.426 \log M_b + \log 1.22, \quad R^2 = 0.98.$$

Table 2. *Ultimate bending strength of small mammalian whole bone specimens loaded in an antero-posterior direction*

Animal	Mean body mass (kg)	Ultimate stress (MN/m ² ± s.d.)			
		Femur	Tibia	Humerus	No
Chipmunk	0.094	263.2 ± 41.7	303.9 ± 49.3	192.5 ± 42.4	4
Ground squirrel	0.137	219.0 ± 23.5	184.6 ± 21.4	171.8 ± 30.3	4
Rat	0.522	253.1 ± 16.5	233.1 ± 32.9	257.5 ± 30.7	12
Kangaroo rat	0.097	210.7 ± 39.4	218.6 ± 33.7	—	8
Totals	—	236.5 ± 37.0	235.1 ± 48.4	219.9 ± 50.7	—

Table 3. *Ultimate bending strength of whole bone specimens from small bipedal birds loaded in an antero-posterior direction*

Animal	Mean body mass (kg)	Ultimate stress (MN/m ² ± s.d.)			No
		Femur	Tibia	Metatarsus	
Painted quail	0.051	311.0 ± 56.8	170.5 ± 36.9	245.2 ± 28.1	4
Bobwhite	0.173	193.3 ± 20.4	294.0 ± 65.7	226.3 ± 52.9	6
Totals	—	252.2 ± 70.7	232.3 ± 83.4	235.8 ± 45.6	—

Table 4. *Ultimate bending strength of bones from large mammals*

Animal	Body mass* (kg)	Bone	Test specimen	Ultimate bending stress (MN/m ² ± s.d.)	Reference
Human	70	Femur	Machined compact bone (wet)	173.5 ± 10.8	Yamada, H. (1973)
		Tibia	Machined compact	199.5 ± 8.7	
		Humerus	Machined compact	190.9 ± 9.6	
Human	70	Tibia	Machined compact	189.1	Dempster & Coleman (1961)
Human	70	Femur	Whole bone (wet)	186.2 ± 4.9	
Horse	400	Femur	Machined compact bone (wet)	186.8 ± 5.5	Yamada, H. (1973)
Cow	700	Femur	Machined compact bone (wet)	264. ± 20.5	Burstein <i>et al.</i> (1972)
Ox	700	?	Machined compact bone (wet)	227	Currey (1976)
Rat	0.35	Femur	Whole bone (wet)	182	Engesaeter, Ekeland & Langeland (1979)
Rat	0.35	Femur	Machined compact bone (dry)†	186.5 ± 33.6	Kimura, Amtmann, Doden & Dyama (1979)

* Approximate adult body weights were taken from E. Walker's 'Animals of the World', 3rd edition, 1975.

† Tested in compression.

second moment of area determined in the present study. The equation for the dashed line and its y-intercept were calculated using a value of 240 MN/m² for the ultimate bending strength of bone from a 1000 kg animal.

Both the present data and the values of ultimate bending strength for large mammals show a fair amount of variability. The variability between different studies is due in

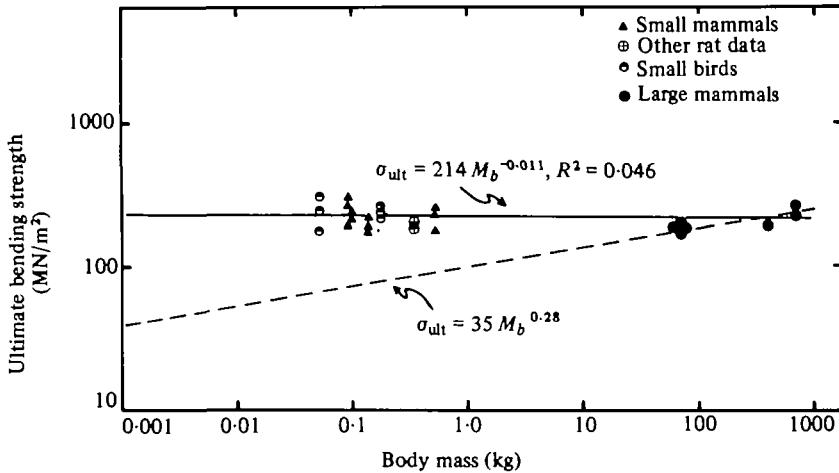


Fig. 4. A graph of the ultimate bending strength of whole bone specimens plotted against body mass on logarithmic co-ordinates. The data for small mammals and bipedal birds are presented along with those for large mammals. The solid line represents the linear regression done on the data for each bone tested within each species. Its slope is not significantly different from zero ($m = -0.011$, $R^2 = 0.046$). The dashed line shows the change in the ultimate bending strength of bone that would be necessary to maintain a uniform safety margin between it and the peak locomotory stress predicted by scaling arguments ($m = 0.28$). The equation was calculated using a value of 240 MN/m^2 for a 1000 kg animal.

part to the different test conditions and specimens used. These are given for each set of data shown. Considering the likelihood of error introduced in the determination of the geometrical parameters necessary to calculate the bending strength of such small bones, as whole test specimens, the values obtained here correlate quite favourably with those reported for more uniform, precisely machined specimens of cortical compact bone from large mammals. The difference between the means of each group of data is not statistically significant ($P > 0.2$), indicated by a slope close to zero for the regression line in Fig. 4.

The slightly higher values of ultimate bending stress obtained in the present study most likely reflect the fact that whole bone specimens were used instead of machined test specimens of compact bone. For a given cross-sectional area, a 'hollow cylinder' characteristic of a whole bone has a larger second moment of area (I) than a solid rod, and will therefore resist greater bending loads. Any initial curvature of the whole bone in the direction in which the bending force was applied will additionally lead to an overestimation of the ultimate bending stress calculated for the tensile cortex where the bones typically fail (Kent, 1946). Finally, the values obtained here, as well as those determined in other studies of the bending strength of compact bone, are larger than what would be expected due to tensile failure alone. Burstein, Currey, Frankel & Reilly (1972) have shown that yielding effects inherent in three-point bending tests result in plastic flow within the tensile and compressive zones of the test specimen, which causes an increase in the ultimate stress measured.

DISCUSSION

The results presented here indicate that the bending strength of vertebrate bone varies little, if any, over a wide range in body size. This would suggest that large animals have much lower safety factors than small animals, given that their skeletons scale geometrically. However, proportionately greater stresses in larger animals could be avoided if the diameter dimensions of their bones increased proportionately more than the linear dimensions.

McMahon (1973, 1975*a*) has recently argued an alternative theory of scaling, 'elastic similarity', which assumes that animals are built to undergo similar elastic deformations in response to gravitational loads. His theory predicts that length scales to diameter to the two-thirds power, or that $l \propto F_w^{0.25}$ and $d \propto F_w^{0.38}$, so that animals become more robust as they increase in size. Accordingly, only a five-fold increase in peak compressive stress ($\sigma_c \propto F_w^{0.24}$) and a two-fold increase in peak bending stress ($\sigma_b \propto F_w^{0.11}$) over a range in size from 1–1000 kg would be predicted to occur. Limb bones of members of the family Bovidae ranging in body mass from 4.4 to 500 kg have been reported to scale according to the predictions of elastic similarity (McMahon, 1975*b*; Alexander, 1977).

However, when a more diverse group of mammals is considered, representing several orders which range in size from 0.003–2500 kg, measurements of length and diameter are found to scale uniformly to body mass (Alexander, Jayes *et al.* 1979), in agreement with the predictions of geometric similarity. Both the measurements of cross-sectional area and second moment of area determined in the present study for eleven species ranging in size from 0.038–276 kg scale closely with the data reported by Alexander, Jayes *et al.* (1979). The allometric proportionalities calculated from our data are $A \propto F_w^{0.72}$ and $I \propto F_w^{1.43}$ compared to $A \propto F_w^{0.72}$ and $I \propto F_w^{1.44}$ derived from their data for diameter. These results indicate that the mammalian skeleton is in fact geometrically similar over a wide range in size, so that a proportionately increased level of stress with body size would be predicted based on bone geometry alone.

Large animals appear to compensate for their bone geometry by proportionately reducing the peak force exerted on the ground as size increases. Alexander (1977) has argued that peak stress scales independently of body mass and has developed a model which predicts that large animals have larger duty factors (defined as the fraction of the stride period that a given limb is in contact with the ground) moving at a given speed than smaller animals. Data for ungulates running at their top speeds (minimum duty factors) show that duty factor scales proportional to $F_w^{0.11}$ for the forelimb and $F_w^{0.14}$ for the hindlimb (Alexander, Langman & Jayes, 1977). Assuming that an inverse relationship exists between peak ground force and duty factor, a proportionately larger duty factor in large animals would mean that they exert peak ground forces that are a lower multiple of their body weight than smaller animals. Recent force-plate data obtained for a variety of different sized animals running or hopping at high speeds indicates that the peak ground force acting on the foot is not a constant multiple of an animal's body weight, but does in fact decrease with increasing size (Cavagna, Heglund & Taylor, 1977). Peak ground forces of up to $3 \times F_w$ and $2.5 \times F_w$ have been measured for a kangaroo rat (0.10 kg) hopping and a chipmunk (0.11 kg)

galloping, respectively, at a steady speed (Heglund, 1979); whereas a horse (300 kg) exerts only about $1.7 \times F_w$ at high speeds (Biewener *et al.* in press). It seems then that the peak forces exerted on the individual limb bones may similarly decrease with increasing size. However, this two-fold difference in peak ground force alone cannot explain the greater than nine-fold difference in peak stress predicted by the empirical data indicative of geometric similarity over this size range.

It seems unreasonable, though, that small animals are built to have much greater safety factors than large animals. For animals to have evolved over such a great range in size, as in mammals, a uniform margin of safety would be expected. The scaling arguments presented here assume that the forces and stresses which are important in affecting bone architecture are those imposed during locomotion at a steady speed. However, it seems likely that small animals may undergo much greater accelerations of their centre of mass during normal activity than large animals. Such accelerations or decelerations may be frequent enough and of significant magnitude to influence the design of the skeleton. Moreover, other features of an animal's skeletal system may affect the force exerted on the limb bones compared to the force exerted at the foot, such as bone curvature and limb orientation relative to the vector of ground force. These aspects of limb morphology along with empirical measurements of *in vivo* stresses developed during locomotion must also be studied to determine whether large animals do in fact operate under lower safety margins than small animals.

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