

ALLOMETRY OF QUADRUPEDAL LOCOMOTION: THE SCALING OF DUTY FACTOR, BONE CURVATURE AND LIMB ORIENTATION TO BODY SIZE

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SUMMARY

1. Measurements of the chord length ($\propto M^{0.31}$) and diameter ($\propto M^{0.35}$) of the femora, tibiae, humeri and radii from 32 species of mammals, ranging in approximate body mass from 0.020–3500 kg, support previous data which show that mammalian long bones scale close to geometric similarity.

2. Scaling of peak stresses based on these measurements of limb bone geometry predicts that peak stress increases $\propto M^{0.28}$, assuming that the forces acting on a bone are directly proportional to an animal's weight.

3. Peak locomotory stresses measured in small and large quadrupeds contradict this scaling prediction, however, showing that the magnitude of peak bone stress is similar over a range of size. Consequently, a uniform safety factor is maintained.

4. Bone curvature ($\propto M^{-0.09}$) and limb bone angle relative to the direction of ground force ($\propto M^{-0.07}$) exhibit a slight, but significant, decrease with increasing body mass.

5. Duty factor measured at the animal's trot–gallop transition speed does not change significantly with body size.

6. The moment arm ratio of ground force to muscular force exerted about a joint was found to decrease dramatically for horses as compared to ground squirrels and chipmunks. This six-fold decrease ($\propto M^{-0.23}$) provides preliminary data which appear to explain, along with the decrease in bone curvature and angle, the similar magnitudes of peak bone stress developed during locomotion in different sized animals.

7. The crouched posture adopted by small quadrupeds while running may allow greater changes in momentum (when accelerating or decelerating) or a decrease in the forces exerted on their limbs.

INTRODUCTION

Recent work has shown that peak stresses of similar magnitude act in the limb bones of different sized mammals during high-speed locomotion. This work has focused

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mainly on steady state locomotion in quadrupeds (Alexander *et al.* 1979; Lanyon & Rubin, 1980; Biewener, Thomason, Goodship & Lanyon, 1983; Biewener, 1983), although measurements of bone stress during bipedal hopping (Alexander & Vernon, 1975), as well as jumping (Alexander, 1974) have also been made. Because large and small animal bones have the same material strength (Biewener, 1982), a fairly uniform safety factor (ratio of fracture stress to peak functional stress) is thus maintained over a range in size.

As animals grow, or increase in size during phylogeny, their anatomical dimensions and physiological parameters increase at different rates. The measurement of how they change with size is the study of allometry. It is generally recognized that if the bones of animals are geometrically similar (i.e. that their lengths increase in direct proportion to their diameters, $l \propto d^{1.0}$), peak stresses acting in them should increase with increasing size. This is because the strength of a bone, or its ability to withstand (compressive) stress, is proportional to its cross-sectional area (l^2), whereas the forces acting on a bone are proportional to some multiple of body weight (l^3). Thus, these forces increase more rapidly than the bone's ability to resist them. McMahon (1973, 1975*a*) has proposed a scaling model, 'elastic similarity', which argues that the linear dimensions of animals do not increase in the same proportion. Instead, according to his model the lengths of structural elements, such as bones, increase in proportion to their diameters (d)¹. In other words, animals become distorted in shape and relatively more stout as they increase in size. This would account, at least in part, for the ability of large animals to maintain a skeletal safety factor similar to much smaller animals. Measurements of the lengths and diameters of ungulate limb bones agree well with elastic similarity ($l \propto d^{0.66}$: McMahon, 1975*b*; $l \propto d^{0.77}$: Alexander, 1977).

However, if the dimensions of mammalian limb bones over a much larger size range (shrew to elephant) are considered, the data show, somewhat surprisingly, that the bones of mammals representing several orders, scale close to geometric similarity ($l \propto d^{0.97}$: Alexander, Jayes, Maloij & Wathuta, 1979). A direct consequence of this, as noted above, is the prediction that peak stress increases significantly with size. Using the allometric relations for bone length and diameter determined by these workers and assuming only that the forces acting on a bone increase in proportion to an animal's body weight, peak stress is predicted to increase proportional to body mass (M)^{0.28} (Biewener, 1982). Therefore, to account for the similar magnitude of peak stress measured in different sized animals, this assumption must be incorrect; larger animals must compensate for the geometric scaling of their bones by reducing the forces acting on the bones of their skeleton. The most effective way to achieve a reduction in peak stress, moreover, is to reduce the bending forces, or net bending moment, exerted on a bone.

If, in addition to the geometric similarity of their skeletal dimensions, the movements of the limbs and trunk of different sized animals during locomotion are also similar, it seems difficult to understand how the forces acting on the limb bones might be reduced in proportion to size. However, if changes in the relative period of support, timing of support, and limb orientation occurred in a regular way with size, then there may be mechanisms to lower the forces and bending moments to which the bones are subjected as size increases.

One mechanism that has been proposed to lower the forces acting on a bone is simply to reduce the peak ground force exerted on the limb during its support phase. This can be accomplished by increasing the relative period of support, or duty factor (D), that a limb provides to the animal during each stride (Alexander, 1977; Biewener, 1983). Duty factor is defined as the fraction of the stride period (T) that a limb is in contact with the ground. Duty factors have been shown to range from greater than 0.5 at walking speeds to less than 0.3 at fast trots and fast gallops (Gambaryan, 1974). By increasing the time over which the impulsive, or time integrated, force ($\int F dt$) is exerted by the limb, the magnitude of peak force can be reduced. This would lead to reduction in both the bending and compressive forces acting on a bone. Alexander (1977) has developed a model which argues that to maintain a uniform stress in the skeleton, large animals have greater duty factors than small animals. This is supported by data obtained from films of ungulates running in the wild (Alexander, Langman & Jayes, 1977). However, the size range of the animals studied was limited, and some accuracy was lost in the measurement of foot contact time because of the difficulty of keeping the animals in a lateral view when being filmed. To measure duty factor more accurately and to confirm whether duty factor increases and contributes to a reduction in peak stress in larger animals, I measured the duty factors of quadrupedal mammals (varying over four orders of magnitude in size) while running on treadmills over a range of gait and speed. The mean duty factor of the fore- and hindlimbs measured at the animals' trot-gallop transition speeds were used to compare duty factor as a function of size. Comparisons were made at this speed because stride frequency at an animal's trot-gallop transition scales regularly with size, as shown by Heglund, Taylor & McMahon (1974), who argued that the trot-gallop transition point represents a 'physiologically equivalent' speed for animals of different size.

In addition to a decrease in magnitude, a reduction in the bending moments exerted by the ground force on the bones of a limb represents a second, and possibly more effective, means by which peak stress could be lowered. This could be accomplished by orientating the bones more closely in the direction of the force, so that they are loaded primarily in axial compression: the loading mode for which bone exhibits the greatest strength (e.g. Burstein, Currey, Frankel & Reilly, 1972). To determine whether this contributes to a reduction in stress, the orientation of the principal fore- and hindlimb bones of the animals were measured midway through the support phase as a function of speed and gait and compared over a range in size at the animals' trot-gallop transition speeds.

Finally, not only are bending or transverse forces important in determining the amount of bending that a bone is subjected to, but the longitudinal curvature inherent in a bone's shape causes axial forces to induce bending moments about the bone's midshaft as well. Frequently, these bending moments are even greater than those exerted due to the transverse force acting on a bone (Biewener *et al.* 1983; Biewener, 1983), which is more commonly thought to be the principal component of bending to which a bone is subjected. Accordingly, if bone curvature were to decrease in a regular way with increasing body size, then this would also represent an important means by which large animals reduce the level of peak stress in their limb bones.

MATERIALS AND METHODS

Glossary of terms used in the text

ζ	characteristic bone curvature
X	moment arm of axial force due to bone curvature measured at the bone's mid-shaft, mm
L	distance from distal end of a bone to its midshaft (equal to one-half the chord length of the bone), mm
D	duty factor
α	limb bone angle to the direction of ground force, degrees
M	body mass, kg
F_w	body weight, N
F_g	ground reaction force, N
F_m	force exerted by muscles, N
F_a	net axial component of force acting on a bone, N
F_t	net transverse component of force acting on a bone, N
R	moment arm of ground force about a joint, mm
r	moment arm of extensor muscles about a joint, mm
c	maximum distance from the neutral plane of bending to the surface of the bone's cortex, mm
A	cross-sectional area of bone at its midshaft, mm ²
I	second moment of area of bone at its midshaft, mm ⁴
σ_c	compressive component of stress, MN/m ²
σ_b	bending component of stress, MN/m ²
l	chord length

Animals

The animals used to measure the scaling of duty factor (D) and limb bone orientation (α) are listed in Table 1. Except for the pocket mouse, at least two individuals

Table 1. *Animals used to determine duty factor (D) and limb bone angle (α)*

Animal	Genus	Body mass (kg)
Pocket mouse	<i>Liomys</i>	0.010
Mouse 1	<i>Mus</i>	0.032
2		0.036
Chipmunk 1	<i>Tamias</i>	0.084
2		0.098
Ground squirrel 1	<i>Spermophilus</i>	0.151
2		0.164
Dog 1	<i>Canis</i>	1.80
2		15.0
3		26.0
4		30.5
Pony 1	<i>Equus</i>	110
2		140
Horse		270

Each species were used in the study. These animals were trained to run on treadmills over a period of several weeks. All of the animals were in good physical condition for the duration of the experiments. The large animals were exercised regularly on the larger of the two treadmills used in the study. The small animals (ground squirrels, chipmunks and mice) were housed in cages with activity wheels. They were run at regular intervals on a small treadmill until it was determined that they had adopted normal patterns of gait over a range of speeds.

Dynamic parameters of gait

Duty factor

To measure duty factor using cine film, it is necessary to film the running animal at a sufficiently high framing rate such that the instants when the feet make contact with and then leave the ground can be accurately determined. The criterion used to establish framing rate was that the foot contact time (t) must be greater than or equal to 15 frames of the film. Generally, runs were analysed with 20–40 frames showing the foot in contact with the ground. An adequately high framing rate is essential for an accurate determination of duty factor. Duty factor, $D = t/T$, where T is the animal's stride period. Because the instants when the foot lands on and then leaves the ground are not precisely known, for the minimum case (where 15 frames show the foot in contact with the ground), the maximum error possible is $2/15$ or 13%. Since a full frame error at the beginning and end of the support phase is unlikely, the error is probably less than this.

The animals were filmed from a lateral view, using a high-speed 16 mm cine camera (Photsonics, 1PL). Animals, whose fur obscured the definition of their joints, had their limbs shaved before filming to allow joint position to be determined more accurately. A 9.5–95 mm F2.2 zoom lens (Angineaux) allowed close-up filming of animals over the entire size range. Framing rates between 200–450 f/s were used for the small animals and 100–350 f/s for the larger ones. Framing rate was determined precisely by a pulse generator which turned on an LED lamp within the camera, marking the edge of the film.

Limb bone angle

The determination of limb bone orientation relative to the vector of ground force was made by measurements of the angles of the different segments of a limb to the vertical, midway through the support phase (Fig. 1A). This method assumes that peak vertical force is exerted midway through the stride and that at this time the horizontal component of force is equal to zero (Fig. 1B). Records of the vertical component of force typically reach a maximum midway through the support phase and can be represented by half of a cycle of a sine wave (Alexander & Jayes, 1978; Biewener *et al.* 1983; Biewener, 1982). The horizontal component of force, similarly, can be represented by a full cycle of a sine wave, whose period is one-half that for vertical force. Thus, when there is a peak in vertical force, the horizontal force passes through zero. This idealized model for the two principal components of ground force acting on a limb is a good representation for bipeds (Alexander & Jayes, 1978) and is fairly characteristic of large quadrupeds (Biewener *et al.* 1983). However, smaller

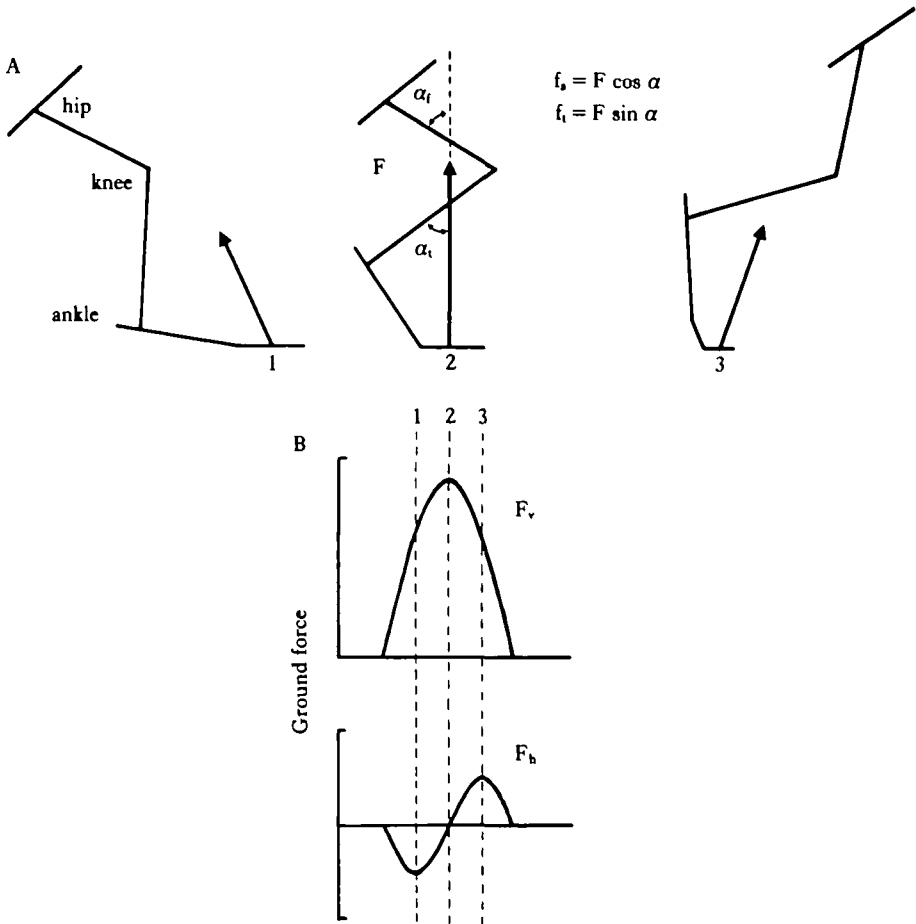


Fig. 1. (A) Schematic representation of hindlimb position and orientation in an animal at three instants during its support phase. The direction and magnitude of the ground force vector (F) is drawn in each case, determined from the vertical (F_v) and horizontal (F_h) components of ground force shown below (B). Units of force are arbitrary. The limb bone angles of the femur (α_f) and tibia (α_t) are indicated for the position of the limb midway through the support phase, corresponding to the instant when peak F_v is exerted and F_h is zero. This was the assumed orientation of ground force for measurements of α in the animals, running at their trot-gallop transition speeds. The axial (f_a) and transverse (f_t) components of the ground force depend on the cosine and sine, respectively, of limb bone angle.

quadrupeds tend to have more skewed records of horizontal force, such that the forelimbs exert a greater decelerating (negative) component of horizontal force and the hindlimbs a greater accelerating (positive) component. As a result, the analysis introduces greater error for the smaller quadrupeds. This is diminished to some extent by the fact that the horizontal component of force is less than 25% of the magnitude of vertical force in most animals. Finally, this measurement further assumes that peak forces and stresses develop coincident with the development of peak vertical force. This is supported by measurements of the stresses and forces acting on various limb bones, made simultaneously with records of ground force in both large and small quadrupeds (Biewener *et al.* 1983; Biewener, 1983).

Bone curvature determined from museum specimens

Measurements of bone curvature were made on the femora, tibiae, humeri and radii of 32 species (four orders) of quadrupedal mammals, ranging in approximate body mass from 0.020–3500 kg, which were housed in the Museum of Comparative Zoology at Harvard University. Body mass, when unknown, was taken as the mean value for the range of mass given by Walker (1975). These estimates may be somewhat unreliable in that Walker generally quotes the largest figures reported for captured or killed animals. The method for the measurement of bone curvature is illustrated in Fig. 2. All of the bones were measured with reference to their lateral aspect. Care was taken to orientate the bones as they are positioned in the animal's limb during locomotion. Modelling clay was used for support. Only adult bone specimens were measured. This was determined by fusion of the epiphyses. Specific reference points on the proximal and distal ends of each bone were used to assure a systematic and unbiased approach for the measurements. Measurements were made using a metric ruler and Vernier calipers. The limb bones from the small animal skeletons (< 2 kg), which were too small to be measured directly, were photographed and then projected with known magnification on to a table before measuring.

Longitudinal bone curvature is defined to represent the moment arm (X) of the axial component of force acting on a bone, which causes this force to exert a bending moment about the bone's midshaft. This moment arm is measured as the orthogonal distance taken from the chord drawn between the proximal and distal ends of the bone to a point midway between the cranial and caudal cortices of the bone at its midshaft. The values of X were normalized to a characteristic length, so that comparison over a range of size could be made. Normalized bone curvature then is:

$$\zeta = \frac{X}{2L} \times 100$$

where 2L is the chord length of a bone.

Moment arm ratio

Because an animal's limb orientation is generally more upright and straightened as size increases, the 'relative mechanical advantage', or moment arm ratio, of extensor muscles *versus* the ground force vector acting about the joints of the limb is argued to increase. If this is true, muscular forces exerted on the bones of larger animals would be reduced. As an initial test of this, records of ground force exerted on the limb synchronized with cine (x-ray cine for the small rodents and light cine for the horses) film records of limb position, which had been obtained in two previous studies (Biewener, 1983; Biewener *et al.* 1983), were used to compare animals of different size. Joint coordinates were digitized using a Vanguard motion analyser and entered into a microcomputer. The orientation and orthogonal distance of the ground force vector (its moment arm) from each joint of the limb was calculated after entering the magnitude of the vertical and horizontal components of ground force for each frame of film. The moment arms of the extensor muscles acting about the limb joints were determined from radiographs of the animals after they had been killed with their limbs

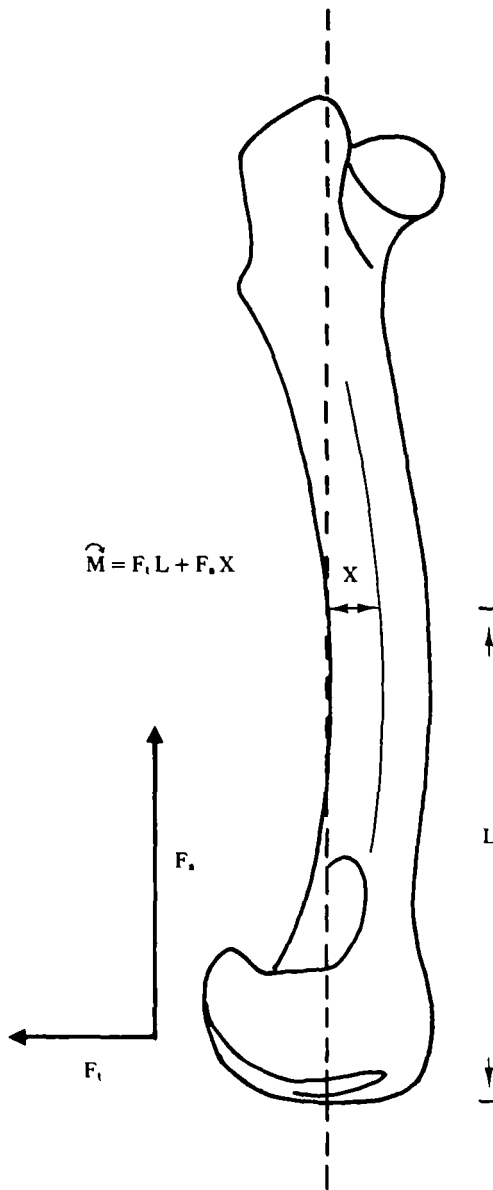


Fig. 2. Tracing of a goat femur to illustrate the method for determining characteristic bone curvature, ζ . Bone curvature is defined to represent the moment arm (X) of the net axial component of force acting on a bone (F_a) which causes F_a to induce a bending moment about the midshaft of the bone. The net bending moment exerted on the bone at its midshaft is calculated to the left. X was measured as the orthogonal distance from the chord drawn between the proximal and distal ends of the bone to the centre of the bone at its midshaft. Characteristic bone curvature, ζ , was calculated as $X/2L \times 100$ to compare the degree of curvature exhibited by bones of different sized animals. Specific reference marks located at a midpoint on the proximal and distal ends of the bone were used to ensure a systematic orientation of the chord drawn for each bone. Femur: (prox.) greater trochanter and (dist.) anterior border of the lateral epicondyle; tibia: (prox.) intercondylar eminences and (dist.) articular groove of the fibula; humerus: (prox.) greater tuberosity and (dist.) centre of rotation of the trochlea; radius: (prox.) centre of rotation of the radial head and (dist.) styloid process.

held in a range of flexed to fully extended positions, and mean values taken. These values were compared with the effective moment arm values measured for the ground forces recorded at fast trots and slow gallops over a force plate; speeds near the trot-gallop transition speed of each animal (no trotting speeds however were obtained for the chipmunks).

Least squares linear regression analysis of the data was used to determine the slope of logarithmic transformed data, or the allometric exponent of the untransformed data, conforming to the form of the equations:

$$\log y = m \log x + \log b$$

$$y = b x^m$$

The 95 % confidence interval of the slope (or exponent), m , the correlation coefficient, R , and standard error of its estimate, *s.e.*, are also presented. The difference between slopes was considered significant when there was no overlap in the 95 % confidence intervals. Variation about the mean is given as \pm *s.d.*

RESULTS

Duty factor

Duty factor decreased curvilinearly with increasing speed in a similar fashion for animals of different size. For each animal, the change in forelimb (Fig. 3A) and hindlimb (Fig. 3B) duty factor with gait and speed was nearly identical. Because the duty factor of an animal's limb at a given speed was found to vary a little, four successive strides at each speed were analysed and the mean values of duty factor for these strides used. The standard deviation about mean duty factor was less than 5 % of the mean. The hindlimbs of smaller quadrupeds typically exhibited greater duty factors than their forelimbs at all three gaits (Table 2). In the larger animals, the difference in duty factor between the fore and hindlimbs was less. At a walk and a trot, fore- and hindlimb duty factors were nearly identical. As the larger quadrupeds change gait from a trot into a gallop, the duty factor of the hindlimb decreases less than that of the forelimb, so that a shift in relative support from the fore- to the hindlimbs is observed. Only for dog 2 was the duty factor of the forelimb consistently greater than that of the hindlimb at each gait. At a gallop, which is an asymmetrical gait as compared to the trot (Hildebrand, 1980), the non-lead fore- and hindlimbs had consistently greater duty factors than the lead fore- and hindlimbs. This was the case for all of the animals in which these measurements were made.

The mean value for the duty factors of the fore- and hindlimbs of each animal at its trot-gallop transition speed (i.e. fastest trot) was used to compare how duty factor varies as a function of size. The trot-gallop transition speeds of the different animals shown in Fig. 3 are denoted by the arrows. A graph of these data on logarithmic coordinates shows that there is little difference in duty factor versus body mass over a range in size from 0.010–270 kg (Fig. 4). The regression of these data yields a slope of -0.006 ± 0.006 ($R = 0.53$, *s.e.* = 0.02), which is not significantly different from zero. The mean duty factor for the fore- and hindlimbs of the different sized animals at their trot-gallop transition speeds is 0.41 ± 0.02 . If the duty factors for the

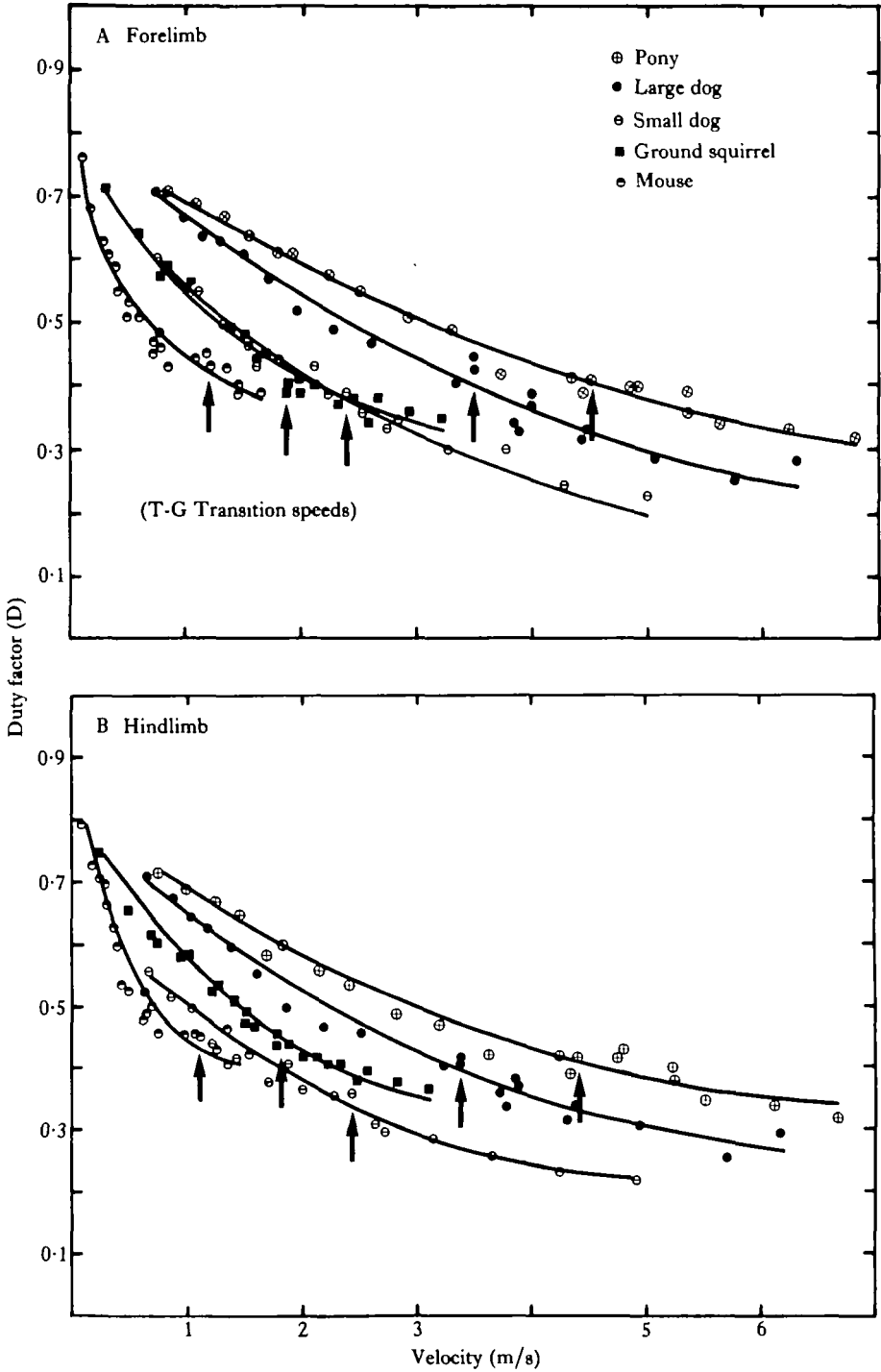


Fig. 3. Graphs of duty factor, D , for (A) the forelimbs and (B) the hindlimbs of different sized quadrupeds plotted against velocity. Duty factor shows a similar curvilinear decrease with increasing velocity for animals of different size. The decrease is not as steep for animals of greater size. No significant difference is observed in the graphs of forelimb D versus hindlimb D as a function of speed and gait within a given animal. The arrows indicate the trot-gallop transition speed of each animal.

Forelimbs and hindlimbs of these animals are considered separately, the regression for the forelimb yields a slope of -0.002 ± 0.006 ($R = 0.58$, s.e. = 0.02), with a mean value for forelimb D of 0.40 ± 0.02 . For the hindlimb the slope is -0.013 ± 0.010 ($R = 0.63$, s.e. = 0.03), with a mean value for hindlimb D of 0.42 ± 0.03 . The slope of the hindlimb is significantly different from zero, whereas the slope for the forelimb is not.

Table 2. Ratio of forelimb duty factor to hindlimb duty factor at each gait

Animal	Mass (kg)	Walk F:H	Trot F:H	Gallop F:H	Fore L:NL	Hind L:N
Pocket mouse	0.010	0.82 (1)	0.88 ± 0.09 (3)	0.77 ± 0.05 (4)		
Mouse	0.032	0.87 ± 0.03 (5)	0.99 ± 0.02 (9)	0.90 ± 0.04 (6)		
Chipmunk	0.086	0.97 (1)	0.96 ± 0.01 (4)	0.95 ± 0.02 (6)		
Ground squirrel	0.151	0.96 (1)	0.95 ± 0.03 (9)	0.95 ± 0.03 (13)	0.98	0.99
Dog 1	1.80	1.07 (1)	1.11 ± 0.03 (7)	1.12 ± 0.08 (10)	0.89	0.98
Dog 2	27.0	0.99 ± 0.01 (5)	1.02 ± 0.04 (7)	0.96 ± 0.04 (9)	0.98	0.95
Pony 1	110	1.00 ± 0.01 (4)	1.02 ± 0.03 (9)	0.96 ± 0.02 (6)	0.96	0.97
Pony 2	140	1.02 (1)	1.05 ± 0.04 (4)	0.93 ± 0.04 (6)	0.96	0.91
Horse	270	1.08 ± 0.02 (4)	1.01 ± 0.06 (7)	0.95 ± 0.03 (7)	0.97	0.98

The non-lead (NL) and lead (L) fore- (F) and hindlimbs (H) of a gallop are given separately. The data are given as the mean \pm s.d. The number of observations are indicated in parentheses.

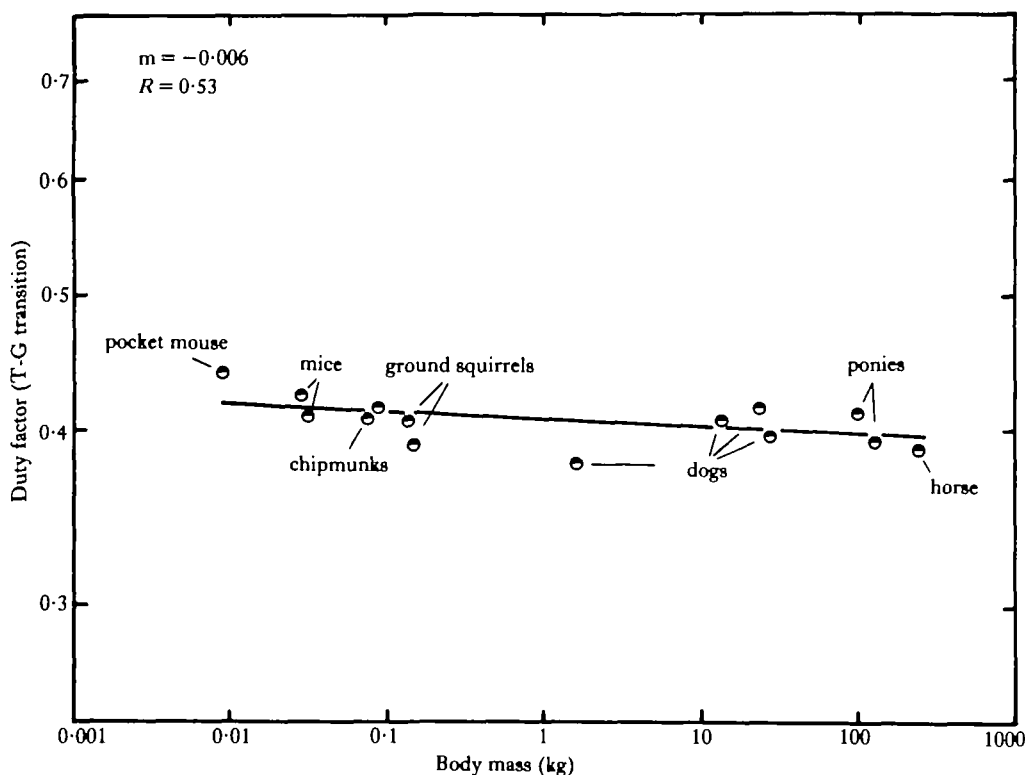


Fig. 4. Mean duty factor (measured at the fastest trotting speed just before the gait transition to a gallop) for the fore- and hindlimbs of different sized quadrupeds plotted against body mass on logarithmic coordinates. The 95% confidence interval for the slope of the line is 0.00 to -0.01 and hence is not significantly different from zero ($R = 0.53$, s.e. = 0.02). The mean value of duty factor over the range in size at the trot-gallop transition speed is 0.41 ± 0.02 .

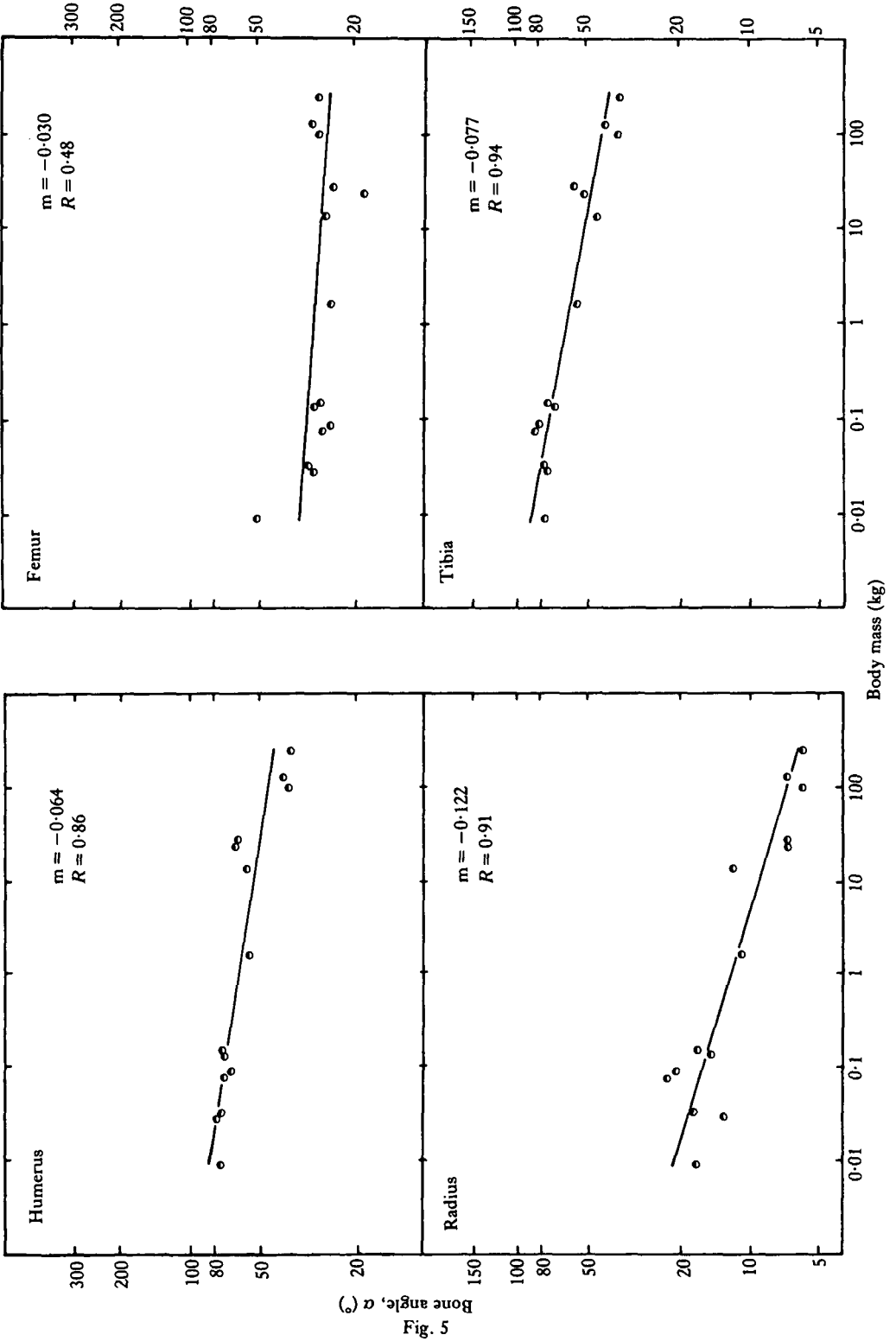


Fig. 5

Limb bone angle

There was a consistent decrease in limb bone orientation to the vertical (α), measured at the animals' trot-gallop transition speeds, with increasing body mass (Fig. 5). Only the slope determined from the regression for femoral angle was not significantly different from zero. The largest decrease was observed in the radius. However, for all of the animals measured, the angle of the radius was the smallest in absolute magnitude. The humerus and tibia were consistently found to be orientated at the largest angle to the (assumed) vertically acting ground force over a range of speed and gait. The mean slope (or allometric exponent) for the four bones combined is -0.073 ± 0.038 .

Bone curvature

Bone curvature exhibited considerable variation as a function of size. The greatest variability was observed in the femora and humeri. The data for the moment arm due to curvature (X), midshaft diameter (d), and chord length (l), which are required to calculate normalized bone curvature (ζ), are presented in Table 3. Bone curvature is plotted against body mass on logarithmic coordinates in Fig. 6. For each bone, ζ decreased slightly with increasing body mass. The greatest decrease in curvature was observed in the humerus and tibia. The radius consistently exhibited the greatest magnitude of curvature over a range of size. Except for the slope of femoral curvature *versus* body mass, the slopes for the three other bones are all significantly different from zero. The mean slope for the four bones combined is -0.086 ± 0.045 .

Bone scaling

For each bone the slope of midshaft diameter versus chord length (plotted on logarithmic coordinates) is slightly greater than one (ranging from 1.10 for the femora to 1.16 for the tibiae, Fig. 7). The mean allometric exponent for the four bones combined is 1.12. Hence, each bone scales close to geometric similarity (a slope of 1.0); the diameters of the bones increasing slightly more than their lengths as size

Fig. 5. Limb bone angle (α), measured midway through the support phase at the animal's trot-gallop transition speed, plotted against body mass on logarithmic coordinates for the femur, tibia, humerus and radius. The slopes of the lines determined from a least squares regression of the data are all significantly different from zero, except the slope of femoral angle. The slope and correlation coefficient are indicated for each bone. The 95 % confidence interval for the slope of each bone is: femur, 0.00 to -0.06; tibia, -0.06 to -0.10; humerus, -0.04 to -0.09; radius, -0.09 to -0.16. The mean slope for the four bones combined is -0.07.

Fig. 6. Normalized bone curvature, ζ , plotted against body mass on logarithmic coordinates for the femora, tibiae, humeri and radii taken from 32 species (four orders) of quadrupedal mammals. A significant decrease in bone curvature with increasing body mass is observed in each bone, except for the femur. The slope and correlation coefficient are shown for each bone. The 95 % confidence interval for the slope of each bone is: femur, +0.05 to -0.14; tibia, -0.03 to -0.19; humerus, -0.02 to -0.27; radius, -0.01 to -0.10. The mean slope for the four bones combined is -0.09.

Fig. 7. Midshaft diameter plotted *versus* (chord) length on logarithmic coordinates for the femora, tibiae, humeri and radii of the 32 species of mammals. The slope of each line is close to 1.0, indicating that the bones scale close to geometric similarity, and are highly significant. The slope and correlation coefficient are shown for each bone. The 95 % confidence interval for the slope of each bone is: femur, 1.16 to 1.04; tibia, 1.23 to 1.09; humerus, 1.19 to 1.05; radius, 1.19 to 1.01.

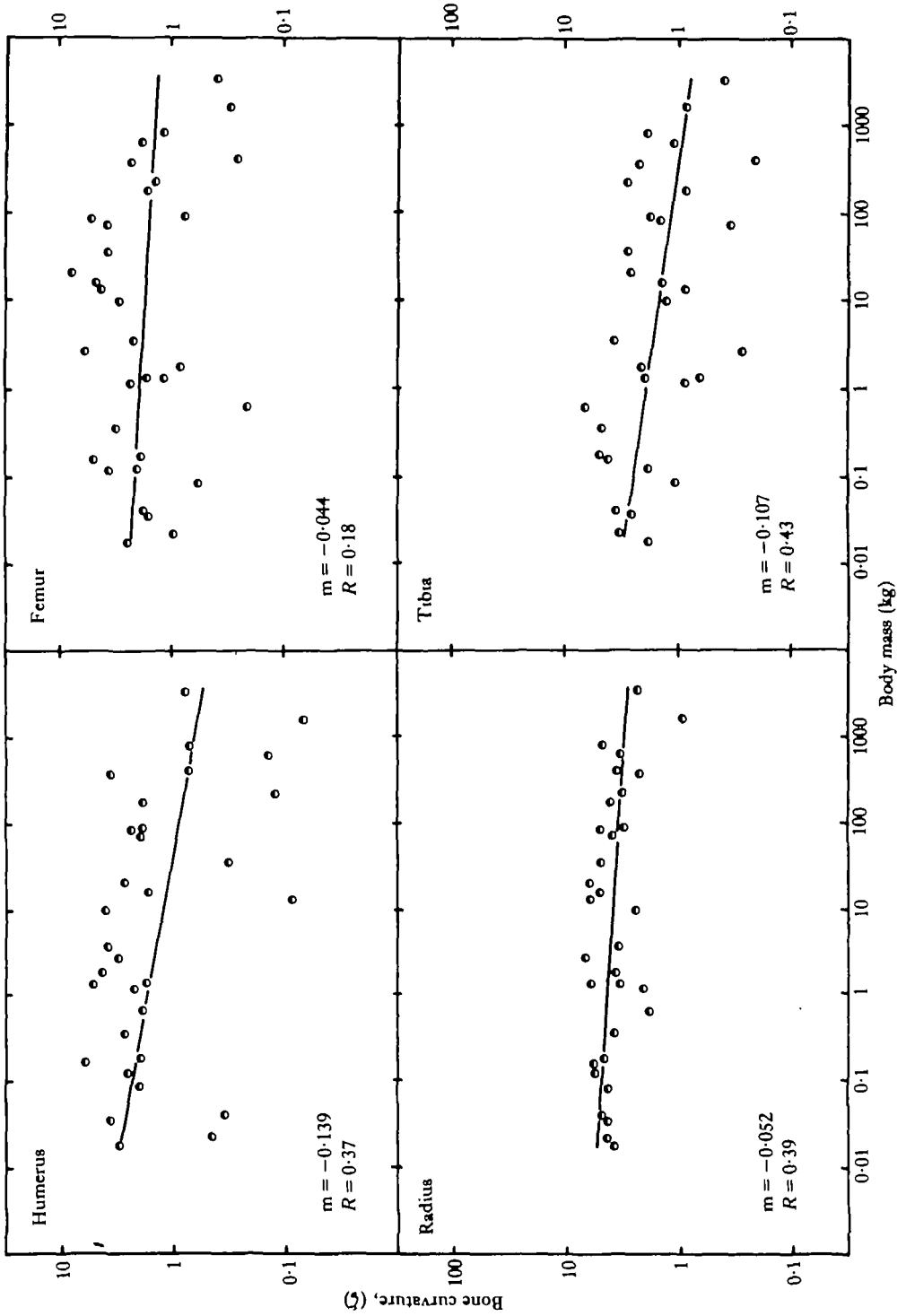


Fig. 6. For legend see p. 159.

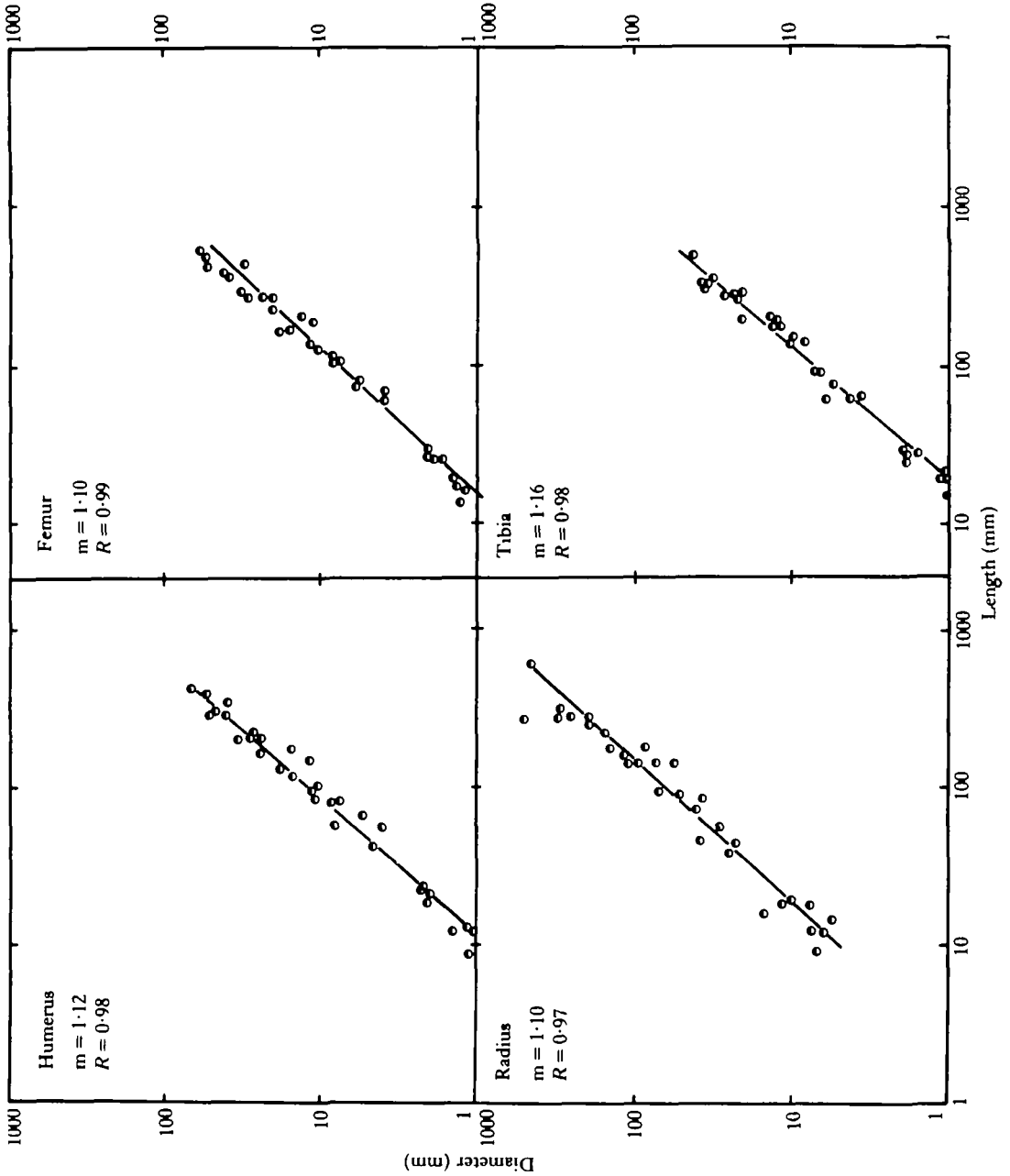


Fig. 7. For legend see p. 159.

Table 3. *Geometrical data measured from the bones of quadrupedal mammals*

Animal	Mass (kg)	Bone	X (mm)	d (mm)	l (mm)
<i>Artiodactyla</i>					
<i>Hippopotamus</i>	3750	femur	2.04	62.1	510
<i>amphibious</i>		tibia	1.48	39.7	346
		humerus	3.27	55.0	411
		radius	7.03	52.6	294
<i>Girrafra</i>	1800	femur	1.49	57.6	473
<i>camelopardalis</i>		tibia	5.04	44.4	527
		humerus	0.36	69.6	442
		radius	5.44	45.4	669
<i>Bos</i>	900	femur	4.40	40.6	359
<i>bison</i>		tibia	7.36	35.7	349
		humerus	2.23	50.1	311
		radius	15.02	31.2	302
<i>Taurotragus</i>	700	femur	7.05	43.7	372
<i>oryx</i>		tibia	4.55	33.5	379
(eland)		humerus	0.41	42.3	302
		radius	10.38	25.3	305
<i>Connochaetes</i>	250	femur	3.91	30.2	268
<i>taurinius</i>		tibia	9.56	24.7	302
(gnu)		humerus	0.26	33.8	215
		radius	9.54	19.1	291
<i>Oryx</i>	200	femur	4.91	33.5	288
<i>gazella</i>		tibia	2.79	28.6	298
(gemsbok)		humerus	3.95	33.7	210
		radius	11.53	19.7	276
<i>Odocoileus</i>	95	femur	15.57	24.4	270
<i>virginianus</i>		tibia	5.12	21.7	315
(deer)		humerus	5.13	29.4	215
		radius	12.34	15.4	239
<i>Capra</i>	80	femur	9.04	21.1	222
<i>hircus</i>		tibia	0.83	14.1	224
(goat)		humerus	3.37	24.9	171
		radius	6.91	11.8	172
<i>Ovis</i>	40	femur	6.33	16.4	166
<i>aries</i>		tibia	6.01	13.6	192
(sheep)		humerus	0.44	18.7	137
		radius	7.91	11.0	153
<i>Gazella</i>	23.5*	femur	14.19	18.9	164
<i>gazella</i>		tibia	6.28	12.6	211
		humerus	3.43	15.3	123
		radius	9.88	9.4	153
<i>Silvicapra</i>	15	femur	6.11	12.3	135
<i>grimmica</i>		tibia	1.34	10.4	151
(duikerbok)		humerus	0.16	11.4	102
		radius	6.47	7.1	102
<i>Madoqua</i>	3.0	femur	7.17	8.6	112
<i>philipsi</i>		tibia	0.38	8.4	156
(dik-dik)		humerus	2.81	8.5	85
		radius	6.89	5.2	96

Animal	Mass (kg)	Bone	X (mm)	d (mm)	l (mm)
Perrisodactyla					
<i>Equus</i>	450*	femur	0.93	56.3	413
<i>callabus</i>		tibia	0.66	39.5	356
(horse)		humerus	2.21	52.5	302
		radius	12.69	30.0	346
Carnivora					
<i>Thalactos</i>	410	femur	10.02	31.9	432
<i>maritimus</i>		tibia	8.14	38.2	327
(polar bear)		humerus	16.48	40.5	365
		radius	7.08	19.8	308
<i>Panthera</i>	100	femur	2.05	20.7	265
<i>onca</i>		tibia	4.10	22.2	216
(jaguar)		humerus	4.41	27.4	233
		radius	6.00	14.4	191
<i>Canis</i>	18.2*	femur	9.96	13.6	203
<i>familiaris</i>		tibia	3.36	13.2	215
(dog)		humerus	3.13	15.7	184
		radius	10.54	8.5	197
<i>Lynx</i>	11	femur	5.76	11.5	188
<i>canadensis</i>		tibia	2.67	12.0	195
(bobcat)		humerus	6.53	11.9	157
		radius	3.82	5.6	154
<i>Nasua</i>	4	femur	2.43	7.6	105
<i>nasua</i>		tibia	4.21	7.2	100
(coati)		humerus	3.54	10.9	90
		radius	2.76	4.0	78
<i>Felis</i>	2.1*	femur	0.91	8.4	106
<i>domesticus</i>		tibia	2.20	6.9	99
(cat)		humerus	3.87	7.8	85
		radius	3.52	3.7	93
<i>Genetta</i>	1.5	femur	0.94	5.9	79
<i>dongalana</i>		tibia	1.79	5.6	83
(genet cat)		humerus	1.22	5.3	70
		radius	2.09	2.9	60
<i>Martes</i>	1.3	femur	2.43	4.0	69
<i>americana</i>		tibia	0.91	3.6	71
(marten)		humerus	2.29	4.0	59
		radius	2.12	2.3	47
<i>Mustella</i>	0.18	femur	1.38	1.69	25.6
<i>nivalis</i>		tibia	1.25	1.87	27.2
(weasel)		humerus	1.56	2.22	24.2
		radius	1.04	1.51	17.1
Rodentia					
<i>Papagomys</i>	1.5	femur	2.15	10.8	125
<i>armandvillei</i>		tibia	1.13	10.1	166
(giant tree rat)		humerus	5.79	10.6	109
		radius	9.72	7.2	154
<i>Marmota</i>	0.70	femur	0.11	6.15	74.1
<i>marmota</i>		tibia	4.89	6.29	67.1
(woodchuck)		humerus	1.14	8.21	59.4
		radius	0.87	3.84	49.6

Thus, according to these data: $l \propto d^{0.89}$. These values are highly significant, with correlation coefficients greater than 0.97.

DISCUSSION

The allometries of bone length and diameter determined in this study are in fairly close agreement with measurements made by Alexander *et al.* (1979). The scaling exponent for length *versus* body mass (0.31) is less than the value of 0.35 determined by these authors, and the exponent for diameter (0.35) is also slightly less than the value of 0.36 which they obtained. One source of error inherent in the present data is the approximation of body mass for most specimens, using values reported by Walker (1975). Frequently these values represent the largest animals killed. This problem is avoided however by scaling the length of a bone to its diameter. The scaling of $l \propto d^{0.89}$ reported here is again closer to the scaling of $l \propto d^{1.0}$ predicted by geometric similarity than to the scaling of $l \propto d^{0.67}$ predicted by McMahon's (1975a) elastic similarity model. Hence, the scaling of bone geometry should promote greater stresses in larger animals. To compensate for this, the results of this study indicate that as animals increase in size, peak stresses are lowered by a general reduction in the curvature and angle of their limb bones relative to the direction of ground force, rather than by an increase in duty factor. The decreases in ζ and α , though not large, are statistically significant. Considerable variation in bone curvature exists, however, within a given size of animals. The particular shape and orientation of a long bone within an animal's limb, although designed to reduce peak stress as a consequence of size scaling, will also reflect adaptation to the specialized range of mechanical activity or movement that the limb must support. Clearly, the curvature of a bone may be due to different, and competing, functional demands placed on an animal's skeleton.

The data reported here, which show no significant increase in duty factor for either the fore- or hindlimb (and, in fact, a significant decrease in hindlimb duty factor for these animals), is in disagreement with the results of Alexander *et al.* (1977), obtained for different sized ungulates running at their top speeds. Their data showed an increase in forelimb duty factor proportional to $M^{0.11}$ (± 0.07) and hindlimb duty factor proportional to $M^{0.14}$ (± 0.09). Instead, the present data agree with previous measurements of the (overall) support period of the forelimbs, as a fraction of stride period, in different sized quadrupeds galloping near their trot-gallop transition speed, for which no significant change was found over the size range of the animals studied (McMahon, 1977). Consistent with these data, and with the possibility that duty factor does not contribute to a significant reduction in the forces acting on the limbs of larger animals, the peak vertical acceleration recorded for the same animals running over a force plate at their trot-gallop transition speed also showed no change with size.

In the present study, the comparison of duty factor as a function of size at the animals' trot-gallop transition speeds was made for two reasons. First, Heglund *et al.* (1974) have argued that the trot-gallop transition speed represents a 'physiologically similar' speed for animals of different size. They found that stride frequency measured at the trot-gallop transition speeds of different sized quadrupeds scaled in a regular way with size, in accordance with elastic similarity. In addition to stride

frequency, McMahon (1975a) later demonstrated a regular scaling (in agreement with elastic similarity) of several other kinematic parameters related to locomotion, measured at the trot-gallop transition point. More recently, Taylor, Heglund & Maloiy (1982) have shown that, at the trot-gallop transition speed, the metabolic cost/step is the same for a series of animals, ranging over more than five orders of magnitude in body mass. Secondly, a comparison of animals moving at their 'top speeds' relies on the assumption that the animals have attained their fastest speeds. This is nearly impossible to establish, especially for animals in the wild.

Because of its proposed link to a reduction in the forces and stresses acting in the limb, the scaling of duty factor at the trot-gallop transition should ideally be correlated to the scaling of peak bone stress at the same speed. Only limited data, however, are available for the scaling of peak bone stress at the trot-gallop transition. Peak stresses measured in the limb bones of ground squirrels at their trot-gallop transition were approximately 50% lower than those recorded in horses: 30 MN/m^2 vs 60 MN/m^2 , respectively (Biewener, 1983; Biewener *et al.* 1983), using a similar method of analysis. Over the size range of these animals, this represents a slight positive allometry for peak stress ($\propto M^{0.09}$). More data must be obtained to establish whether in fact peak stress developed at the trot-gallop transition point scales independently of body mass.

The different scaling relationships determined for duty factor in these two studies, however, would not appear to be the result of a comparison of animals running at their trot-gallop transition speeds *versus* those which are estimated to be at their top speeds. As the graphs in Fig. 3 show, duty factor decreases curvilinearly with increasing speed, so that at very high galloping speeds the decrease in duty factor is only slight. Thus, the values of duty factor measured here at the highest galloping speed of the animal are unlikely to be much lower than those measured at its 'top speed'. Minimum duty factors recorded in the dogs (0.28) and small horses (0.30) at 7.0 m/s in the present study, however, are significantly greater than duty factors of 0.18 to 0.20 measured by Alexander *et al.* (1977) for various ungulates at their highest speeds (10–14 m/s). Because of the relatively low framing rates used by these workers (64 f/s), at very high speeds and at stride periods as low as 0.30 s, errors as great as 30% could arise in their measurement of duty factor. If the values of duty factor measured at the top galloping speed of each animal in the present study are used to compare duty factor as a function of size, the regression equations determined from these data yield slopes of -0.02 ± 0.02 for the forelimb and -0.04 ± 0.03 for the hindlimb, which are not significantly different from the values obtained for the data at their trot-gallop transition speeds but are significantly different from the values reported by Alexander *et al.* (1977). The different scaling relationships presented by these two studies also cannot be due to differences in duty factor measured at a fast trot *versus* a gallop because no discernible change occurred at the gait transition, except for a slight difference between the non-lead and lead limbs. Finally, considering that the animals had been trained for several weeks prior to the experiments, differences due to running on treadmills, as opposed to running over ground, are also not believed to be significant. Moreover, the former approach has the advantages of an accurate determination of running speed and the interval of ground contact time, as well as the other parameters of gait measured in this study.

A correlation appears to exist, however, between duty factor and foot length. The animals studied here represent different mammalian orders and a greater size range than the ungulates studied by Alexander and his colleagues. The smaller quadrupeds (rodents), especially the pocket mouse, have enlarged hind feet compared to their fore feet. The consistently greater duty factors of the hindlimbs versus the forelimbs of these smaller quadrupeds correlates with a longer length of the foot in contact with the ground during the support phase of the limb. This suggests that the relative length of the foot in contact with the ground may, in part, determine the duty factor of the limb. These animals, as well as the dogs, are digitigrade. Horses, in contrast, are unguligrade (stand on their toes). The comparatively short length of the 'foot' in contact with the ground in horses might be expected, therefore, to reduce the duty factor of its limbs; countering the tendency for an increase due to large body size. As a result, the data obtained in this study shows a slight decrease in fore- and hindlimb duty factor when comparing horses, dogs and rodents. However, within a group of animals whose appendicular skeleton is similar, such as ungulates, the negative effect introduced by reduced 'foot' length would not be important, so that an increase in duty factor might be found.

The slightly greater duty factors measured for the non-lead, as opposed to the lead, fore- and hindlimbs at low-speed gallops is somewhat surprising, because *in vivo* stresses measured in the radius and metacarpus of the horse (Biewener *et al.* 1983) as well as in the tibiae of ponies and dogs (Lanyon & Rubin, 1980) show peak stresses to be significantly lower in the lead limb bones (10–20 %) compared to the non-lead limb bones. The larger duty factors measured for the non-lead fore- and hindlimbs would be expected to result in the development of a lower level of stress because of the increased time over which force is exerted on the ground. However, the greater magnitude of ground force and stress acting in the non-lead limb indicates that this is not the case. Rather, the difference in stress magnitude may be due to the phase relationship of the two limbs. The non-lead limb is the first to land from the aerial phase which precedes the support phases of the contralateral fore- or hind limbs (Hildebrand, 1980) and thus may absorb more of the impact resulting from the transfer of the animal's weight.

The allometric relationship for limb bone angle ($\alpha \propto M^{-0.07}$) agrees fairly well with the scaling of limb excursion angle ($\propto M^{-0.10}$) reported by McMahon (1975a). Measurements of forelimb and hindlimb excursion angles of the animals filmed in this study and compared at their trot–gallop transition speeds show the same decrease in limb excursion angle with increasing size. The slope for the forelimb was -0.10 ± 0.02 ($R = 0.95$), ranging from 123° in the pocket mouse to 43° in the horse. The slope for the hindlimb was -0.08 ± 0.02 ($R = 0.93$), ranging from 103° in the pocket mouse to 38° in the horse. Elastic similarity would predict angular excursions $\propto M^{-0.125}$ because of the scale-dependent increased mechanical advantage (l/d) of larger animals, whereas for geometrically similar animals, the excursion angles of their limbs and limb segments should be scale independent ($\propto M^{0.0}$). Consequently, although limb bone geometry scales close to geometric similarity, kinematic parameters related to gait (stride frequency and limb excursion angle) appear to scale in agreement with elastic similarity.

Considered together, the negative allometry for limb bone angle and bone curvature

(ζ) $\propto M^{-0.09}$ do not account for the observation that peak locomotory stresses scale independently of body mass. Based on empirical data for the length, diameter and cross-sectional geometry of the limb bones of mammals varying widely in size, Biewener (1982) recently argued that peak stress would be predicted to increase $\propto M^{0.28}$, assuming that the axial (compressive) and transverse (bending) forces acting on an animal's bones are directly proportional to the animal's body weight (F_w). The two equations used to calculate the peak stresses due to compression and bending are:

$$\sigma_c = -\frac{F_a}{A} \quad (1)$$

$$\text{and } \sigma_b = \pm \frac{[(F_t L) + (F_a X)] c}{I} \quad (2)$$

where σ_c is the compressive component of stress, σ_b is the bending component of stress, F_a is the axial component of force acting on the bone, F_t is the transverse component of force acting on the bone, L is the distance from the distal end of the bone to its midshaft, X is the moment arm due to bone curvature, c is the maximum distance from the neutral plane of bending to the surface of the bone's cortex, A is the bone's cross-sectional area at its midshaft, and I is the second moment of area at its midshaft.

The negative allometry of bone curvature *versus* body mass affects the second bending moment term in equation 2 ($F_a X$), whereas the negative allometry of limb bone angle affects the first bending moment term in equation 2 ($F_t L$). It was initially assumed that F_a and $F_t \propto M^{1.0}$ (Biewener, 1982). Given that L and $X \propto M^{0.35}$, according to the results of Alexander *et al.* (1979), each bending moment term scales proportional to $M^{1.35}$. Incorporating the results of the present study, the allometry for limb bone angle reduces the scaling of $F_t \propto M^{0.93}$, so that $(F_t L)$ scales proportional to $M^{1.28}$; whereas the allometry for bone curvature reduces the scaling of $X \propto M^{0.26}$, so that $(F_a X)$ scales proportional to $M^{1.26}$. Because these two terms are summed in equation 2, rather than taken as a product, the mean scaling effect of bone curvature and limb bone angle is to reduce the predicted scaling exponent of σ_b *versus* body weight from 0.28 to 0.20. Over the size range from a 0.10 kg chipmunk to a 300 kg horse, this would account for 50% of the reduction in stress due to bending. σ_b , then, would still be predicted to increase five-fold. Neither parameter significantly affects the scaling of σ_c . The relative decrease in limb bone angle, which reduces F_t , does lead to a slight increase in F_a . However, it is unlikely that this increase is very large because of the greater mechanical advantage of the ground force relative to the extensor muscles acting about the joints of the limb (Alexander, 1974; Alexander & Vernon, 1975; Biewener, 1983). Because of this, the net axial component of force acting on the bone (F_a) is primarily due to the axial component of the muscular force exerted on the bone, rather than the axial component of the ground force.

However, if the ratio of the moment arm (R) of the ground force to the moment arm (r) of the force exerted by the extensor muscles decreases in a regular way with increasing size, $R/r \propto 1/M$, then the muscular forces exerted on the limb bones of larger animals would be reduced in proportion to their weight. In other words, a substantial reduction in muscular force can be achieved simply by increasing the

mechanical advantage of the muscles relative to the ground force acting about the joints of the limb. A schematic representation of this is shown in Fig. 8. The limb drawn to the left typifies a small quadruped, such as a ground squirrel, whereas the limb drawn to the right is drawn from the forelimb of a horse. With the limb held in a more upright, straightened position and aligned close to the direction of ground force (Fig. 8B), the moments exerted by the ground force (in this case, the elbow) are reduced significantly as compared to those exerted about the joints of the limb shown in Fig. 8A.

Data for the moment arm ratio, or 'relative mechanical advantage', of muscles acting about the different joints of the forelimb and hindlimb of two quadrupedal rodents and a horse are presented in Table 5. These data show that the relative mechanical advantage of extensor muscles is consistently lower for the joints of the larger animal. The mean ratio for the different joints measured is 6.1 ± 2.1 . If the data for these animals are consistent over this size range, they would represent a scaling proportional to $M^{-0.23}$. Clearly, additional data must be obtained for animals of different sizes to substantiate this suggestion. Because muscular forces decrease in direct proportion to the moment arm ratio, these forces are reduced six-fold in horses compared to chipmunks. Muscles, in general, appear to be aligned close to the longitudinal axis of the bone (Biewener *et al.* 1983; Biewener, 1983). Thus, a reduction

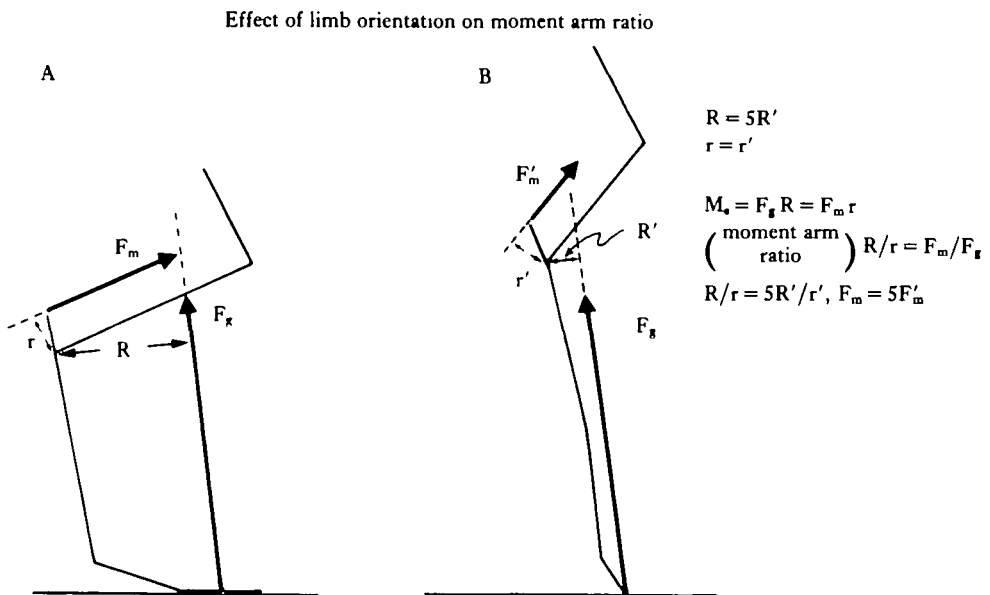


Fig. 8. A schematic representation of the forelimb configuration characteristic of a ground squirrel, which adopts a crouched posture, *versus* that of a horse, which is relatively straight and more upright, to illustrate the effect of limb orientation on the moment arm ratio at the elbow. The moment arm (R) of the vector of ground force (F_g) acting at the elbow of limb A is five times as great as the moment arm (R') of the same ground force vector acting about the elbow of limb B. Given that the extensor muscles, which exert forces F_m and F'_m , respectively, to counteract the moment exerted by the ground force (M_e), have the same mechanical advantage in either limb ($r = r'$), the moment arm ratio of limb A is thus five times greater than limb B. Equating the opposing moments exerted by the ground force and muscular force about the elbow, we see that a five-fold reduction in moment arm ratio ($R/r = 5R'/r'$) leads to a proportionate reduction in the forces exerted by the muscles on the bone (in this case, the humerus). Note that the magnitude of the vectors, F_m and F'_m , are not drawn to scale.

Table 5. *Moment arm ratio (R/r) for the joints of the forelimb and hindlimb of two rodents and a horse*

Animal	F _w (N)	FORELIMB			No.
		Wrist	Elbow	Shoulder	
Chipmunk	0.94	7.6 ± 0.7	7.3 ± 2.1	20.5 ± 8.5	6
Ground squirrel	1.34	11.9 ± 2.8	9.4 ± 2.2	27.0 ± 11.1	6
Horse	2600	2.3 ± 0.8	1.8 ± 1.2	3.6 ± 1.7	7
		HINDLIMB			
		Ankle	Knee	Hip	
Chipmunk		13.6 ± 3.2	17.0 ± 6.1	5.9 ± 6.9	6
Ground squirrel		6.7 ± 3.1	7.7 ± 5.3	10.4 ± 6.3	6
Horse		1.4 ± 0.4	1.3 ± 0.7	1.8 ± 0.6	7

Values given are the mean ± s.d.

in the level of force they exert will most strongly affect F_a rather than F_t . Because of bone curvature, however, this would also result in a reduction of the bending moment exerted on the bone, as well as the level of compressive stress that it is subjected to. If this scaling proportionality held for animals over a range of size, this would account for 85% of the reduction in stress that is predicted based on bone geometry alone [i.e. peak stress $\propto (M^{-0.23} M^{0.28}) = M^{0.05}$, rather than $M^{0.28}$]. The exponent of -0.23 , derived from an admittedly small sample size, at least indicates that this effect, due to differences in limb orientation as a function of size, deserves more attention and may explain the similar magnitudes of peak stress developed in the limb bones of different sized animals during locomotion.

The question arises, however, as to why small animals (quadrupeds) are more 'crouched' while running and large animals are not? A tentative explanation may be that the crouched posture adopted by small quadrupeds represents a compromise between greater bone stress (hence the need for increased bone tissue) *versus* the ability to change momentum rapidly without having to increase the forces exerted on the limb. Predators are usually larger than their prey, and it is commonly observed that small animals are capable of greater changes in speed, as well as direction, than are larger animals. These are useful strategies for escaping from a larger, less agile foe. With a crouched limb posture while running, the animal's hip (or shoulder) height is reduced relative to the sum of the lengths of its limb segments. However, its maximum effective hip height (when the limb is fully extended) is greater than during steady speed locomotion. The importance of this is that it provides a greater interval of time (dt) over which force (F) can be exerted on the ground to thrust the animal into the air; so that the magnitude of force exerted is reduced for a given change in momentum. Alternatively, if the level of force remains the same, an increase in dt will result in an increase in $\int F dt$ (impulsive force). In this latter situation, rather than decreasing force, the animal is able to increase its final momentum when leaving the ground. An analogous situation is that of a person who crouches down, flexing his (or her) hips, knees and ankles, before jumping to achieve a greater height.

Larger animals, on the other hand, are incapable of achieving such rapid changes in velocity without significantly increasing the force exerted on the ground. (In th

case where they fall or land from a jump, velocity decreases quickly, but peak force increases substantially, frequently enough to fracture a bone or rupture a tendon.) By having increased their effective limb length, straightening out their limb segments and increasing the length of distal limb elements, large animals not only decrease the net axial and transverse forces acting on their skeleton, as we have seen, but increase the top speeds which they can attain. Faster steady state speeds and lower forces, however, compromise an ability to change direction and speed rapidly.

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