

LOCOMOTORY STRESSES IN THE LIMB BONES OF TWO SMALL MAMMALS: THE GROUND SQUIRREL AND CHIPMUNK

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SUMMARY

Peak stresses acting in limb bones should increase with increasing size if the forces acting on the bones increase in direct proportion to the animal's body weight. This is a direct consequence of the scaling of limb bone geometry over a wide range in size in mammals. In addition, recent work has shown that the material strength of bone is similar in large and small animals. If the assumptions in this analysis are correct, large animals would have a lower safety factor to failure than small animals. The purpose of this study was to measure peak stresses acting in the limb bones of small animals during locomotion and compare the results with similar measurements available for larger animals. Locomotory stresses acting in the fore and hindlimb bones of two rodents, the ground squirrel (*Spermophilus tridecemlineatus*) and chipmunk (*Tamias striatus*), were calculated using ground force recordings and measurements of limb position taken from high speed x-ray cine films. Peak (compressive) stresses calculated to act in the bones of these animals (-31 to -86 MN/m²) are similar in magnitude to those determined for much larger mammals. The more proximal bones of the fore and hindlimb, the humerus and femur, were found to develop stresses (-31 to -42 MN/m²) significantly lower than those acting in the more distal bones of each limb: the radius, ulna and tibia (-58 to -86 MN/m²). All of the long bones from both species, except their femora, were found to be loaded principally in bending. The caudal cortices of each bone developed a peak compressive stress, whereas the cranial cortices were loaded in tension. Various features of the musculo-skeletal organization and manner of locomotion in these rodents are considered to explain how animals of different size maintain a uniform safety factor to failure.

INTRODUCTION

Body size and locomotion necessarily play important roles in the design of an animal's skeleton. Size is important because of the effects of scale. Changes in the dimensions of the bones of the skeleton must accompany large increases in body size so that the increased forces can be supported safely. Locomotion probably places the greatest demand on an animal's skeleton in terms of mechanical stress and therefore affects the orientation and shape of bones and the organization of muscles exerting

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force on them. In addition, it seems clear that large size also constrains an animal's locomotory repertoire. Animals the size of horses do not leap into trees, as do cats, or run and climb with the agility of squirrels. Because the animal's skeleton must regularly resist the forces imposed during locomotion, it seems likely that skeletal design will reflect the need to support those forces effectively. In order to identify the factors influencing skeletal morphology, the dynamic forces acting on a bone and the stresses which they produce, must be considered.

Recent data show that over a very broad range in size, from a shrew to an elephant, mammals scale close to geometric similarity (Alexander, Jayes, Maloiy & Wathuta, 1979). It has been suggested from these results that larger animals develop greater peak stresses in their bones than do small animals (Biewener, 1982). However, if locomotory performance is limited because of large size, so that the forces exerted on a limb are reduced, the increases in stress that would occur simply due to bone geometry might be compensated for. In fact, Alexander (1977) has developed a model which predicts that peak locomotory stress scales independent of body size. This model holds that peak ground forces, and hence the forces acting on a bone, must decrease (relative to body weight) with increasing size for peak stress to remain constant. Measurements of bone stress in large mammals (Alexander, 1974; Alexander & Vernon, 1975; Biewener, Thomason, Goodship & Lanyon, 1983) indicate that peak (compressive) stresses as high as -80 to -110 MN/m² may be achieved during galloping or jumping. This would mean that these animals operate with a safety factor (ratio of fracture stress to peak functional stress) of about two to three. However, measurements of the stress developed in the bones of small animals when moving at high speeds have not yet been made.

To determine whether peak stress is independent of body size or whether small animals develop dynamic stresses significantly lower than large animals, I have measured the stresses acting in the principal fore and hindlimb bones of two rodents, the ground squirrel and chipmunk. Comparisons are made between the loading conditions of the different bones within the appendicular skeleton of these two animals to illustrate and emphasize the importance of the influence of bone curvature and limb orientation on the resultant magnitude and distribution of stress observed within the cortices of the bones. The results are then compared with published data available for much larger animals to identify those features of the musculo-skeletal organization and manner of locomotion most affected by changes in size.

MATERIALS AND METHODS

Simultaneous x-ray cine films and force plate recordings were made of two ground squirrels, (*Spermophilus tridecemlineatus*), body mass: 112 and 137 g, and two chipmunks (*Tamias striatus*), body mass: 92 and 96 g. The animals were housed in cages with activity wheels and had free access to a commercially available rat diet and water. The animals were in good physical condition throughout the experiments. Because of their small size, x-ray cinematography was required to determine accurately bone and joint position during locomotion.

The force plate was similar in design to that recently described by Heglund (1981). The force plate uses strain gauges in a Wheatstone bridge circuit to give separa-

Itage outputs proportional to the vertical and horizontal (longitudinal) components of the force acting on it, with less than 3% cross-talk between components. The natural frequencies are 170 Hz in the vertical and 240 Hz in the horizontal directions. These levels were high enough to determine accurately the components of force exerted on the limb for any frame of the film. The force plate was calibrated with known weights before and after a series of experiments were completed. Force output was uniform over the entire surface of the plate (3% variation, worst case), and the responses were linear over the range of forces recorded. The outputs were recorded on magnetic tape (Bell & Howell, CPR-4100) and subsequently run off on a chart recorder (Gould, model 260).

The animals were trained to run over the force plate, located midway in an enclosed track 4.3 m in length. The surfaces of the track and force plate were coated with a mixture of paint and sand to minimize slipping. Most of the track was constructed of wood, except the walls along the sides of the force plate, which were made of cardboard to facilitate transmission of x-rays and a sharper contrast of the animal's skeleton.

X-ray cine films were taken from a lateral projection as the animals ran over the force plate, using Siemens Tridoros 150 G-3 equipment. Framing rates of 135–150 f/s were used. A signal from the camera's shutter was recorded on the magnetic tape and played off on the chart recorder for synchronization with the records of force. A Vanguard motion analyser was used to analyse the films. The coordinates of the joints were digitized and entered into a microprocessor along with the vertical (F_v) and horizontal (F_h) components of the force for each frame of film. Velocity was determined by measuring the distance that the animal travelled across the field of the camera versus time. The animals' velocity was difficult to control, as they were unrestrained when running down the track. Only in the ground squirrels were trotting speeds obtained. For the most part, however, galloping speeds were recorded and analysed. Ten replicate measurements of joint position for both the fore and hindlimbs of a ground squirrel were made for one run to assess the variability inherent in the determination of joint position. Standard deviations were determined for the coordinates of each joint and found to range from ± 0.38 mm for the elbow to ± 0.99 mm for the shoulder in the forelimb and from ± 0.41 mm for the ankle to ± 1.03 mm for the knee in the hindlimb.

At a trot, forces were recorded when one fore or hindlimb landed and was isolated on the force plate. At a gallop, forces were recorded and analysed for both hindlimbs together. Typically they landed simultaneously, and the forces were assumed to be equally distributed between the two limbs. Forces were also recorded when both forelimbs landed together at a gallop (full bound; Howell, 1944), again assuming equal distribution of force between them. When the support phases of the forelimbs were out of phase with one another, the run was not analysed. More frequently, however, the animals used a half bound, so that a single forelimb was isolated on the plate. These runs were analysed as well.

The ground reaction force was also assumed to act at a mid-point between the ends of the foot (or hand) which was in contact with the ground. This assumption probably introduces little error in the case of the forelimb because of the relatively small size of the carpus. In the case of the hindlimb, the foot is longer and the chance of error is greater. However, relatively early in the support phase, before peak force is exerted

on the ground, the metatarsals rotate off the ground so that only the phalanges remain in contact; thereby reducing the magnitude of error introduced.

Once the film and force recordings were completed the animals were killed. Measurements of the moment arms of muscles about joints were made from radiographs taken of the animals' limbs in different positions. Anatomical measurements of the muscles and bones required to calculate bone stress were also made, and the sites of origin and insertion of the muscles noted. The data obtained from these measurements are presented in Table 1 for the bones and in Table 2 for the muscles of each animal. Mean cross-sectional area of the muscles was determined as described by Alexander (1977), using a value of 1060 kg/m^3 for the density of striated muscle (Gong, Arnold & Cohn, 1964).

To calculate the stresses acting in a limb bone, it is first necessary to determine the moments exerted by the ground force about the joints of the limb, based on the magnitude and orientation of the ground force with respect to the position of the limb at a given instant in time. The forces exerted by the muscles or muscle group to counteract these moments can then be determined, knowing their mechanical advantage (moment arm) about each joint. In the present analysis no antagonistic activity was assumed. This agrees with electromyographic data for rat forearm muscles (Cohen & Gans, 1976). Comparable data for the hindlimb are not available. If the muscles acting about a given joint have different lines of action (e.g. the action of the hamstrings and adductor femoris on the femur), the force is considered to be

Table 1. *Anatomical data for the forelimb and hindlimb bones*

Animal	Bone	A (mm^2)	l (mm^4)	c (mm)	x (mm)	L (mm)	r (mm)
ground sq. # 1 (137 g)	humerus	2.21	0.92	1.09	3.40	11.3	0.30
	radius	0.69	0.09	0.36	1.20	9.7	1.00
	ulna	0.91	0.10	0.56	1.20	11.4	0.30
	femur	2.04	0.82	1.05	2.03	13.2	0.50
	tibia (fibula)	1.12 0.11)	0.30	0.80	3.94	15.3	0.40
ground sq. # 2 (112 g)	humerus	2.05	0.87	1.00	3.27	11.4	0.30
	radius	0.64	0.10	0.38	1.20	9.6	0.90
	ulna	0.89	0.09	0.53	1.20	10.9	0.30
	femur	1.69	0.72	0.95	2.00	13.1	0.40
	tibia (fibula)	1.07 0.12)	0.25	0.82	3.90	15.1	0.30
chipmunk # 1 (92 g)	humerus	2.12	0.74	1.05	3.00	9.8	0
	radius	0.85	0.11	0.58	1.18	9.8	0.70
	ulna	0.58	0.09	0.55	1.18	11.2	0.20
	femur	1.74	0.73	0.98	2.00	12.8	0
	tibia (fibula)	1.56 0.13)	0.55	0.96	2.80	15.0	0
chipmunk # 2 (96 g)	humerus	1.98	0.77	1.01	2.90	9.7	0
	radius	0.81	0.10	0.61	1.16	9.6	0.80
	ulna	0.67	0.09	0.59	1.16	10.9	0.30
	femur	1.79	0.78	0.95	2.10	12.8	0
	tibia (fibula)	1.59 0.16)	0.62	0.98	2.70	14.9	0

Table 2. Anatomical data for the mean fibre cross-sectional area and angle of the muscles of the forelimb and hindlimb to the bone's longitudinal axis. The angles (α) are determined in the cranio-caudal plane

Forelimb muscles	Ground squirrel				Chipmunk			
	# 1		# 2		# 1		# 2	
	A (mm ²)/ α (°)		A / α		A / α		A / α	
Triceps (long head)	26.0	2	31.1	3	50.1	3	42.0	2
(lateral head)	6.4	15	6.6	16	13.8	12	12.3	12
(medial head)		17	5.1	15	8.4	16	9.6	14
Carpal flexors	45.1	6	40.6	4	40.7	5	38.3	4
Hindlimb muscles								
Quadriceps	68.4	0	74.0	0	123.7	0	112.6	0
Biceps femoris (main)	6.3	7.5	7.8	7	14.8	5	16.2	5.5
(accessory)	3.6	4	3.3	4	15.9	6	13.6	7
Semimembranosus	5.3	7.5	5.9	7	12.5	5	11.3	5.5
Semitendinosus	4.5	4	5.0	4	5.2	6	5.6	7
Adductor femoris	17.7	10	16.8	8	25.1	10	23.9	10.5
Gastrocnemius	51.5	1	42.5	2	84.3	1	63.1	0
Plantaris	13.8	1	15.2	2	23.0	1	22.1	0
Soleus	6.8	6	11.1	6	4.1	5	6.3	6

distributed between the muscles in proportion to their fibre cross-sectional area. In other words, equal stress is assumed to act in each muscle. Having calculated all the forces acting on a given bone, the net axial (F_a) and transverse (F_t) components of force, as well as the net bending moment, acting on the bone can be determined. Inertial forces due to angular or linear accelerations of the limb segments were not calculated and were considered to be relatively insignificant.

Because it is impossible to determine the proportion of force exerted by different muscles acting about a joint (only the total force required to exert the reaction moment is known), if the extensor muscles have different lines of action, assumptions of how the total force is distributed between individual muscles will necessarily introduce error in the calculation of the net axial and transverse forces acting on the bone. Where the lines of action of the muscles are nearly the same, the error is small. However, in the case of the humerus and femur of these rodents, differences in the orientation of muscles exerting force on them (by as much as 16°) pose a potential source of error. To evaluate this, a 'worst-case' calculation of stress was made for the fore and hindlimb bones of each animal based on data obtained for a single run. A comparison of the stresses, calculated assuming that all the force is exerted by the muscle (or muscles) acting at the greatest angle to the bone's longitudinal axis, is expressed as a percentage of the stresses calculated using the assumption adopted in this study: that equal stress acts in the different muscles. In the chipmunk forelimb, a worst-case error of 6% (low) was obtained for the radius and ulna and 26% (high) for the humerus. In the chipmunk hindlimb, the worst-case error calculated for the tibia was 13% (high), and for the femur it was 18% (low). The potential errors calculated for the limb bones of the ground squirrel were all less than those calculated for the chipmunk, because of the closer orientation of muscles exerting force and/or a smaller size of muscle aligned furthest from the bone's longitudinal axis (e.g. the medial and

lateral heads versus the long head of the triceps, Table 2). It should be noted that available electromyographic evidence for other animals while trotting and galloping (Cohen & Gans, 1976; Rasmussen, Chan & Goslow, 1978; Tokuriki, 1973, 1974; Goslow *et al.* 1981) indicates that, within a given extensor group, it is unlikely that all of the force is exerted by only one muscle or a portion of a muscle. Recent data obtained for muscle activity based on glycogen depletion (Sullivan & Armstrong, 1978) show, however, that as rats increase speed, there is a progressive increase in activity of more peripheral regions of the triceps surae group (acting about the ankle). Nevertheless, given that the more centrally located muscles remain active at the higher speeds, the assumption that equal stress acts in different muscles seems reasonable. Consequently, the source of error introduced is probably not nearly as great as the values calculated above.

A drawing of the ground squirrel tibia and the forces which act on it during the support phase are shown in Fig. 1. The forces exerted by the plantar flexor muscles (P) to counteract the moment exerted by the ground force about the ankle (M_a) are

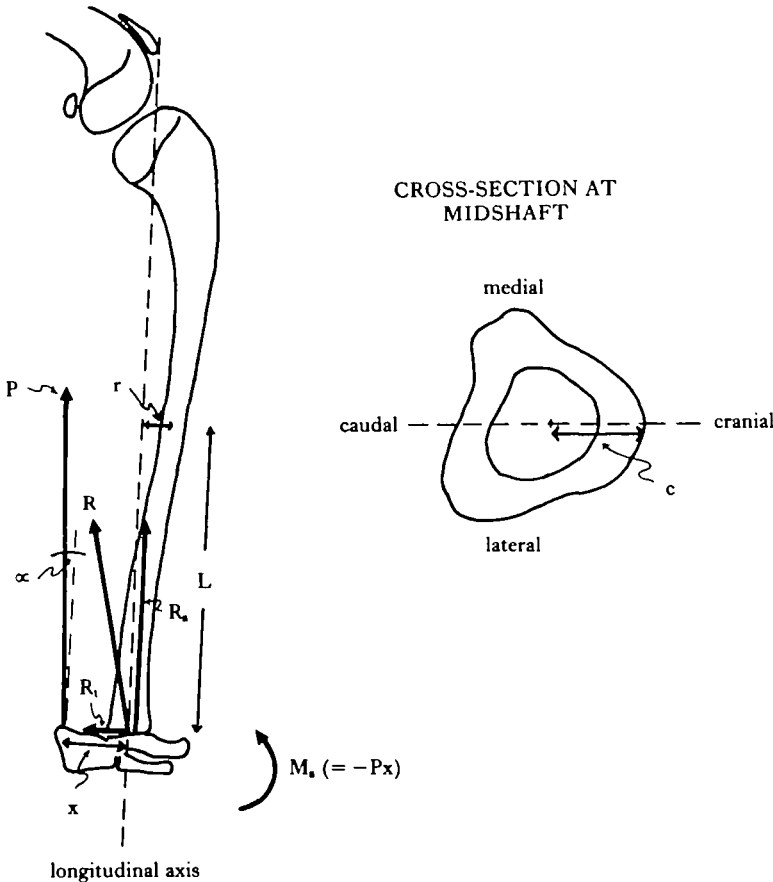


Fig. 1. Schematic drawing of loading in the ground squirrel tibia, illustrating the method of analysis for calculating stress at the bone's midshaft. The force exerted by the muscles (P) acting about the ankle has been simplified to be acting in only one direction for purposes of clarity. The midshaft cross-sectional geometry of the tibia and method for determining the parameter c are shown to the right.

indicated along with their moment arm (x). The stress due to axial compression is then given by:

$$\sigma_c = - \frac{P(\cos\alpha) + R_a}{A} \quad (1)$$

where A is the cross-sectional area of the tibia at its midshaft, α is the angle of the line of action of the flexor muscles to the bone's longitudinal axis, and R_a is the axial component of the ground force acting on the bone. The stress due to bending is given by:

$$\sigma_b = \pm \frac{[(R_t + P(\sin\alpha))L + (P(\cos\alpha) + R_a)r]c}{I} \quad (2)$$

where I is the second moment of area (for bending in the antero-posterior direction) at the midshaft of the bone, L is the moment arm of the transverse components of the ground force (R_t) and the flexor muscles about the midshaft, r is the moment arm of the axial components of the ground force (R_a) and the flexors about the midshaft due to bone curvature, and c is the distance from the neutral plane of bending to the surface of the cortex. Bending in a 'positive' direction is defined here to indicate a tensile (positive) stress acting in the cranial cortex of the bone and a compressive (negative) stress acting in its caudal cortex. The analysis described here is similar to that of Alexander (1974), except that it accounts for the curvature of each bone and uses the actual cross-sectional geometry of the bone to determine A and I at the midshaft, rather than assuming an ideal geometrical shape. The measurement of r was made directly from radiographs. It represents the distance taken from the midpoint of 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. The measurements of A and I were made from photographs of bone cross-sections at the midshaft which were magnified a known amount and traced along their endosteal and periosteal surfaces, using a digitizing table to enter the geometric data into the microprocessor. The calculations of bone stress were computed using the microprocessor, after entering the appropriate anatomical data.

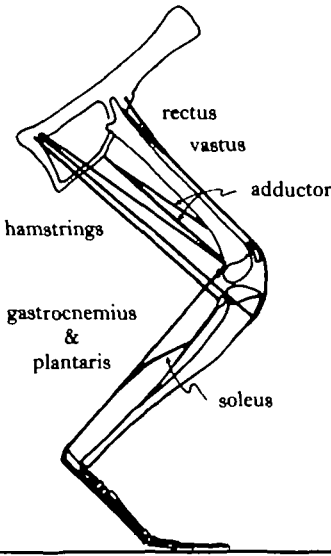
RESULTS

Forelimb anatomy

The skeletal relations of the ground squirrel forelimb are similar to those of the chipmunk and are shown in Fig. 2B. The muscles that are relevant to an analysis of the stresses acting in the humerus, radius, and ulna are included as well, illustrating their lines of action. The carpal flexors, which are active during the support phase to counteract the moment exerted by the ground force about the carpus, arise from the medial epicondyle of the humerus (flexor carpi radialis and ulnaris), as well as the proximo-caudal third of the radius and ulna (flexor digitorum superficialis and profundus, respectively). These four muscles act approximately along the same line, closely parallel to the longitudinal axis of the radius and ulna, and insert on the carpals and phalanges. Accordingly, they exert mainly an axial force on the radius and ulna. The tendons of the digital flexor muscles pass over the carpus to insert on the metacarpals. In doing so, they exert a flexor moment about the carpus, as well as the

GROUND SQUIRREL

A hindlimb



B forelimb

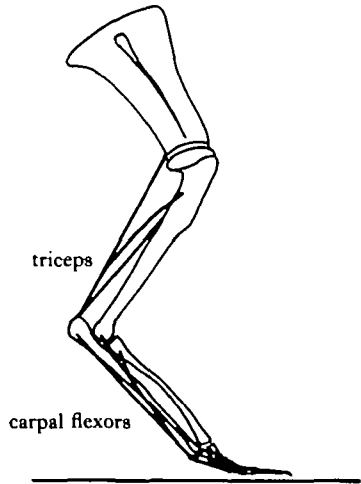


Fig. 2. (A) Hindlimb and (B) forelimb anatomy of the ground squirrel. The heavy lines represent the line of action of the muscles assumed to be exerting force during the support phase, as well as their points of origin and insertion on the skeleton.

metacarpo-phalangeal and interphalangeal joints. There is a narrow range of medial deviation in the orientation of these muscles, with the flexor carpi ulnaris orientated the furthest medially (9°) and flexor carpi radialis the least ($<2^\circ$). This will result in some medial bending, but whereas the orientation of peak stress will be shifted slightly in a medial direction, the magnitude of peak stress calculated in the midshaft cortices of these bones will not be affected significantly. To calculate the stresses acting in the radius and ulna, it is assumed that the forces are equally distributed between each bone. Consequently, differences in the distribution of stress calculated to be acting within the cortices of each bone reflect differences in their cross-sectional geometry and degree of curvature. Whereas the ulnae of these rodents are fairly straight along their lengths, the radii possess prominent concave curvatures along their caudal aspects (Table 1).


The muscle that must be active during the support phase to counteract the flexor moment exerted about the elbow is the triceps. This muscle consists of a long head which arises mainly from the posterior aspect of the glenoid cavity on the scapula, a lateral head which arises from the proximo-lateral third of the humerus, and a medial head which arises from the caudal aspect of the humerus, distal to the radial line. The long head is much larger than the medial and lateral heads of the triceps in both species. The triceps has a common tendon of insertion, attaching to the olecranon process of the ulna. The lateral and medial heads of the triceps are orientated at a fairly large angle to the humerus ($12\text{--}17^\circ$) in both species. The long head, however, is more closely aligned (3°) to the bone's longitudinal axis. Consequently, the force exerted by the triceps loads the humerus primarily in axial compression, and only slightly in bending.

Hindlimb anatomy

The skeletal morphology of the ground squirrel hindlimb is shown in Fig. 2A and, again, is similar to the chipmunk hindlimb. The muscles that must be considered to determine the stresses acting in the femur and tibia are included, illustrating their lines of action. The plantar flexor muscles, which are active to counteract the extensor moment exerted by the ground reaction force about the ankle (dorsi-flexion) during the support phase, arise via sesamoids from the medial and lateral epicondyles of the femur (medial and lateral gastrocnemius, respectively, and plantaris). The much smaller soleus arises from the proximo-caudal fifth of the fibula. These muscles have a common tendon of insertion which attaches to the calcaneus. The plantaris tendon passes under the calcaneus to insert on the proximal phalanges and thus exerts a flexor moment about the metatarso-phalangeal joint as well. The medial and lateral gastrocnemius comprise the major mass (and fibre area; Table 2) of muscle within this group in both species. The soleus is quite small. The lines of action of these muscles are closely parallel to the longitudinal axis of the tibia. Consequently, they exert primarily an axial force on the tibia. In each species the fibula is a very slender bone compared to the tibia (Table 1). In calculating the stress in the tibia, the fibula was ignored as a load-bearing element. This introduces an overestimation of the stress calculated to act in the tibia which may be as much as 10%.

The muscles that exert force on the femur during the support phase are more complex in their arrangement. The quadriceps musculature must be active to counteract the flexor moment exerted by the ground force about the knee. This flexor moment is augmented by not only the action of the hamstring muscles about the knee, which are active to extend the hip, but also the action of the gastrocnemius about the knee. The quadriceps take origin from the inferior iliac spine (rectus femoris) and the proximo-cranial third of the femur (vasti). This muscle group has a common tendon of insertion on the patella, which connects via the patellar tendon to the cranial tibial crest. The hamstrings arise from the ischium and attach on the patella and cranial tibial crest (biceps femoris), as well as the medial epicondyle of the femur and the proximo-medial aspect of the tibia (semimembranosus and semitendinosus, respectively). The adductor femoris is also active in these animals as a hip extensor during the support phase. This muscle arises from a broad origin on the pubic ramus and inserts along the distal-medial third of the femur. To calculate the stresses acting in the femur it was assumed that the angles of the various muscles exerting force on the femur do not change significantly during the support phase. The angle changes at the hip ($<30^\circ$) and at the knee ($<20^\circ$) are small. Moreover, the adductor and hamstrings are at angles of less than 11° and 7.5° to the femur in both species, so that only small changes in their orientation are likely to occur.

*Limb orientation, ground forces, and bone stress**Forelimb*

When the forelimb lands on the ground during a trot, and especially at a gallop, it acts to decelerate the animal's forward velocity (note the large negative component in  record of horizontal force, F_h , in Fig. 3). The increase in the magnitude of the

decelerating component of F_h when each animal changes gait from a trot to a gallop is due to the aerial phase, or extended suspension (Hildebrand, 1980), that is introduced between the support phases of the hindlimbs (which throw the animal into the aerial phase) and the forelimbs (which land from the aerial phase) from one stride to the next. This aerial phase generally increases as speed increases during a gallop (unpublished data) and correlates with an increase in the negative component of F_h .

The peak magnitude of the vertical component of force (F_v) acting on the forelimb is greater than that acting on the hindlimb. This is the case for larger animals as well (Jayes & Alexander, 1978; Biewener *et al.* 1983) and may be consistent over a range of size, although the difference in peak F_v exerted by the forelimb versus the hindlimb is not as great in the larger animals. At high speed gallops, peak F_v exerted by the chipmunk forelimb can be as much as 50 % greater than that exerted by the hindlimb. In the ground squirrel, as much as 30 % difference is observed.

The radius and ulna are closely aligned with the direction of the ground force throughout the stride ($0-9^\circ$) in both species (Fig. 3A), suggesting that these bones are loaded primarily in compression. In contrast, the humerus is loaded as much as 75° from the direction of the ground force, indicating that it is loaded principally in bending. Calculation of the stresses acting in the cortices of these bones shows, however, that all three bones are loaded primarily in bending, acting to place the

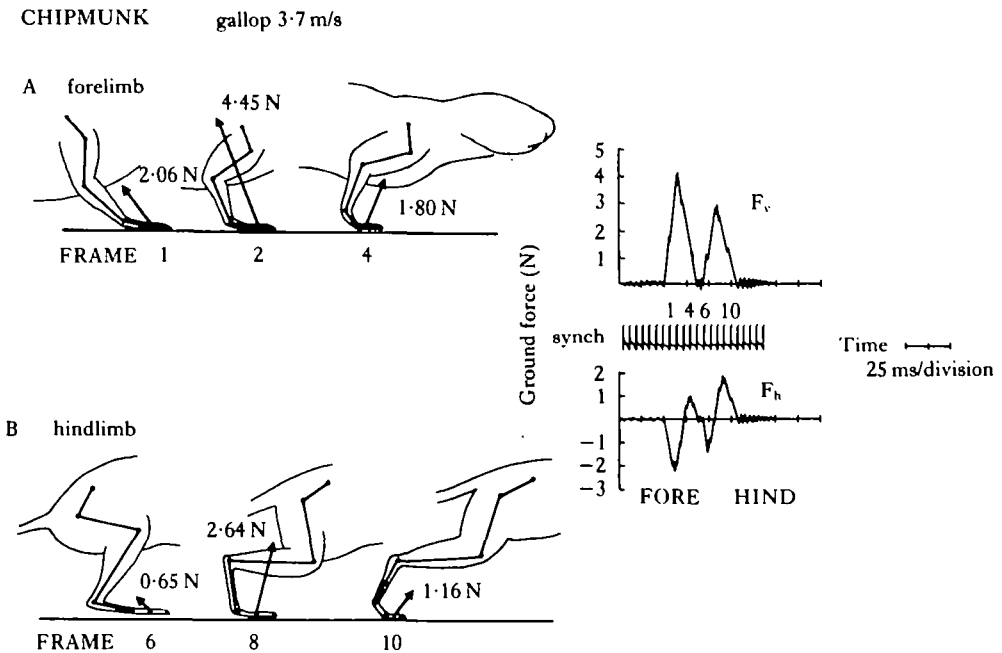


Fig. 3. Representative drawing of the (A) forelimb and (B) hindlimb position of a chipmunk galloping at 3.7 m/s. Three different positions are shown for each limb during its respective support phase, corresponding to three frames of the film. The records of the vertical (F_v) and horizontal (F_h) components of the ground reaction force exerted by the fore, and then the hindlimb, along with the trace of the camera synch pulse, are also shown. The resultant vector of ground force is drawn in for each frame indicated, illustrating its orientation with respect to the fore and hindlimb bones. Note that in this case the forces shown are for the two forelimbs and hindlimbs together. The forces were assumed to be equally distributed between each limb, in the calculation of bone stress.

■anial cortices in tension and the caudal cortices in compression (Figs 4A, 5A). Correspondingly, the bending component of stress (σ_b) is greater than the compressive component of stress (σ_c) in each bone. The magnitude of peak stress is greatest in the caudal cortices due to the orientation of bending. This loading situation is observed at both a trot and a gallop.

Despite their close alignment to the direction of the ground force, the distal forelimb bones are loaded in bending because of their caudal, concave curvature. This curvature induces a large bending moment about the midshaft of each bone (see Fig. 1), exerted by the axial components of the ground force (R_a) and the carpal flexors. Because the ulna of each species is less curved than the radius (Table 1), the magnitude of bending induced in it is less. In a sense, these bending moments can be viewed as acting to 'bow' each bone out cranially; much as tightening a bowstring bends a bow to a greater extent.

At a gallop, the bending moment induced in the radius by its curvature is, in fact, nearly four times greater than that due to the net transverse force (F_t) acting at the distal end of each bone (6.5 Nmm versus 1.8 Nmm, respectively). Even though the

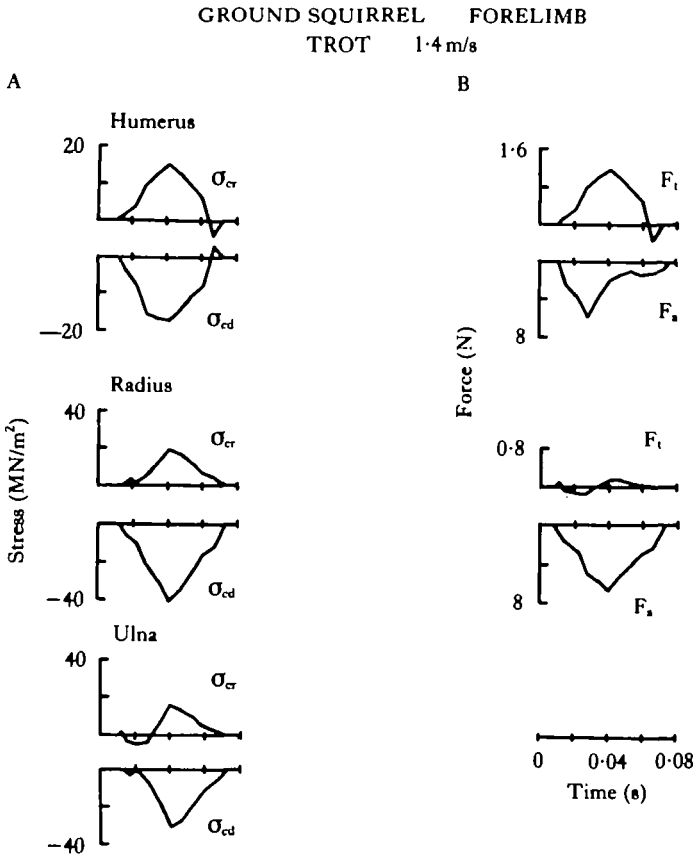


Fig. 4. Representative records of (A) longitudinal stress calculated to be acting in the midshaft cranial (σ_{cr}) and caudal (σ_{cd}) cortices of each forelimb bone of the ground squirrel at a trot. (B) The net transverse (F_t) and axial (F_a) components of force acting on each bone are shown to the right. Note the different scale of force for F_t versus F_a .

A. A. BIEWENER
GROUND SQUIRREL FORELIMB
GALLOP 2.6 m/s

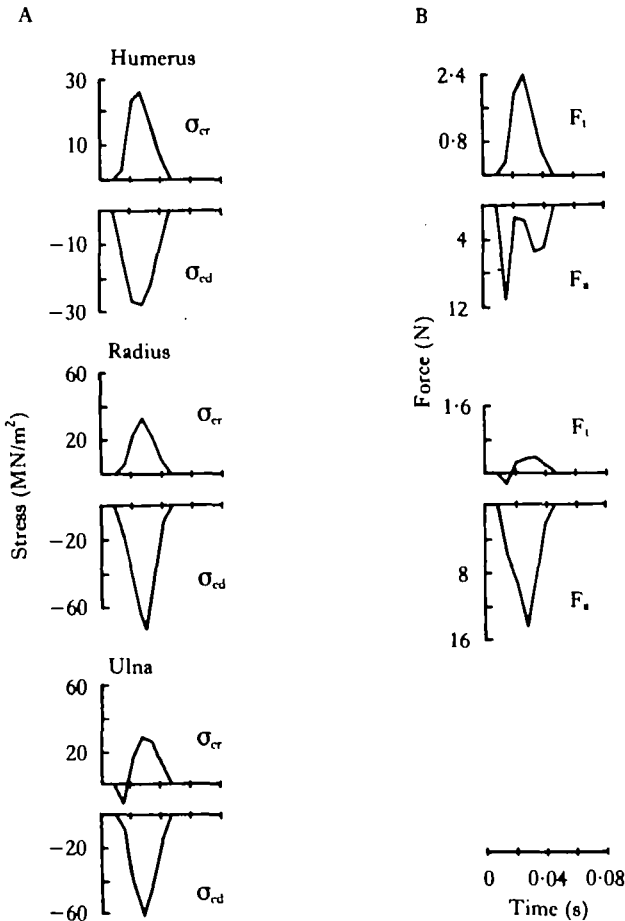


Fig. 5. Representative records of (A) longitudinal stress calculated for the midshaft cranial and caudal cortices of each forelimb bone of a ground squirrel at a gallop. (B) Net transverse and axial components of force acting on each bone.

moment arm (r) due to bone curvature is much smaller (11 times) than the moment arm (L) of F_t , the peak magnitude of F_a is more than 40 times greater than F_t at a trot and a gallop. These bending moments are not always additive. At the beginning of the support phase of a trot, F_t swings negative (Figs 4B, 5B), indicating bending exerted in the cranial direction. This is counteracted by the bending induced by the bone's curvature. During the second half of the support phase, F_t swings positive so that the bending moments exerted about the bone's midshaft are additive.

When the foot first lands on the ground at a trot and a gallop, the ulna is initially loaded in compression. Midway through the support phase, bending increases sufficiently to place the cranial cortex in tension. Because the ulna is less curved and is therefore subjected to less bending than the radius, the peak magnitude of stress developed in its cortices is less than in the radius. Peak stress generally occurs mid-

Through the support phase in both the radius and ulna of each species at a trot and gallop, coincident with the peak in the vertical component of force exerted on the ground.

The humerus of each species is a relatively straight, robust bone. It is orientated at a large angle to the direction of ground force throughout the support phase. As a result, the bending observed in it is due to the large transverse component of force acting on it. As in the radius and ulna, development of peak stress in each of its cortices occurs midway through the support phase of both gaits. The magnitude of peak stress in the humerus, however, is significantly less than that developed in either the radius or ulna because of its larger size and lack of curvature. This was consistent over the range of speeds and gaits observed. Similarly, in the chipmunk peak stress in the humerus was lower than in the radius and ulna at a gallop.

Hindlimb

In contrast to the forelimbs, which exert a net decelerating force on the ground, the hindlimbs of the ground squirrel and chipmunk exert a net accelerating force (note the large positive component of the horizontal force, F_h , in Fig. 3) when moving at a steady speed. As the ground squirrel changes gait from a trot to a gallop, the accelerating component of F_h increases, corresponding to the increase in the decelerating component of F_h exerted by the forelimbs. At a gallop, the orientation of the chipmunk tibia is at a large angle to the direction of the ground force throughout the support phase ($38\text{--}62^\circ$), suggesting that it is loaded mainly in bending. The femur is also orientated at a fairly large angle to the direction of the ground force ($15\text{--}28^\circ$), indicating that it, too, is subjected to a significant level of bending. The same orientation of loading is observed in the tibia and femur of the ground squirrel.

Calculation of the stresses acting in the cranial and caudal cortices of the tibia of each species show it to be loaded in bending throughout the support phase at both a trot and gallop (Figs 6A, 7A). As in the forelimb bones, bending is orientated to place the cranial cortex in tension and the caudal cortex in compression. The femora of both species however are loaded in overall compression. Correspondingly, the compressive component of stress (σ_c) is typically greater than the bending component of stress (σ_b) in these bones. In the ground squirrel femur bending is positive, so that peak stress acts in the caudal cortex. This is in contrast to what would be expected from the bone's orientation during the support phase. By comparison, and as expected from its position during the support phase, the net orientation of bending in the chipmunk femur is negative (not shown). Accordingly, peak stress acts in its cranial, rather than its caudal cortex.

Bending in the ground squirrel tibia is primarily the result of the transverse component of force acting at its distal end and, to a lesser extent, the axial component of force acting about the curvature at its midshaft. The bone has a slight 'S'-shaped curvature along the distal two-thirds of its length, where it becomes slender relative to its proximal end. The more prominent curvature exists at the midshaft and is concave with respect to its caudal aspect. Consequently, the bending moments exerted by F_t and F_a are additive, as they are in the radius and ulna of the forearm. The chipmunk tibia, in contrast, is relatively straight. Bending in it arises strictly as a consequence of the transverse force acting about its midshaft. The difference in the

A. A. BIEWENER
GROUND SQUIRREL HINDLIMB
TROT 1.3 m/s

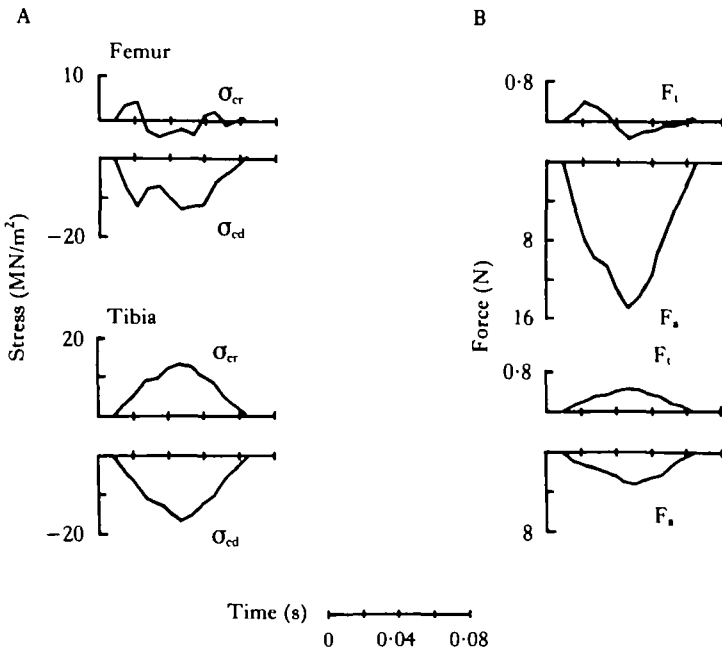


Fig. 6. (A) Longitudinal stresses acting in the hindlimb bones of a ground squirrel at a trot. (B) Net transverse and axial components of force acting on each bone. Note the different scale of force for F_t versus F_a .

degree of curvature of the tibiae of these two species correlates with a consistently lower magnitude of stress calculated to be acting in the chipmunk versus the ground squirrel tibia over the range of speeds recorded (Fig. 9). At a trot, peak stress acts in the ground squirrel tibia midway through the support phase, coinciding with a peak in the vertical component of the ground force (Figs 3, 6A). However at a gallop, peak stress develops earlier in the support phase, before a peak in F_v occurs (Fig. 7A).

The femora of the ground squirrel and chipmunk are robust in comparison to their tibiae. This is consistent with the greater mass of the humerus compared to the radius and ulna of the forelimb. The increased mass (as well as A and I) of the more proximal limb bones may correlate with the greater mass of musculature exerting force on them and/or a greater surface area necessary for sites of attachment for muscles and tendons to the bones. Whereas the ground squirrel femur possesses a slight concave curvature along its caudal aspect, the chipmunk femur, like the tibia, is relatively straight. The predominant force exerted by the muscles acting on the femur of each species is compressive. The adductor and hamstring muscles do contribute, however, to a significant transverse force exerted in the caudal direction. The magnitude of force they exert is largely dependent on the moment they must exert to extend the hip. The adductor femoris is medially ($<10^\circ$), as well as caudally, orientated to the femur. The medial bending that results from its action has been neglected in the present analysis. Its effect would be to shift the axes of the stresses acting in the cranial and cau-

GROUND SQUIRREL HINDLIMB
GALLOP 2.8 m/s

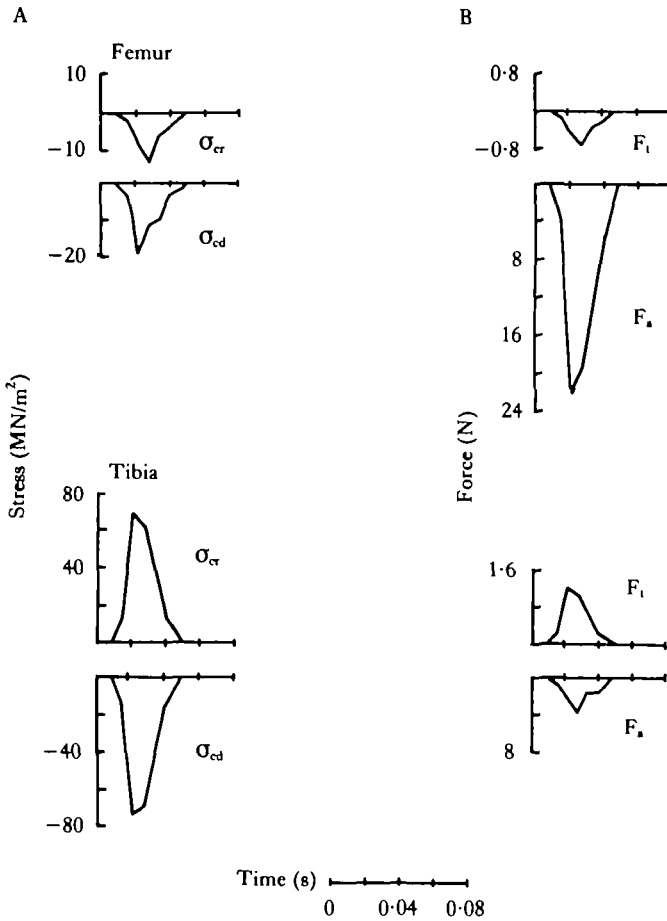


Fig. 7. (A) Longitudinal stresses acting in the hindlimb bones of a ground squirrel at a gallop. (B) Net transverse and axial components of force acting on each bone.

cortices medially, rather than greatly altering the magnitude of stress acting in these cortices.

In the ground squirrel, the bending moment exerted by the transverse components of force of the adductor and hamstring muscles is augmented by the bending moment induced by F_a acting about the bone's curvature. These two (positive) bending moments combined are greater than that exerted by the transverse component of the ground force (R_t) in the opposite direction. Consequently, because the net bending moment exerted on the femur is in the caudal direction, peak stress acts in the caudal cortex. This loading situation is generally consistent over the range of speeds observed. As in the tibia, peak stress develops in the femur midway through the support phase at a trot, but occurs earlier at a gallop. The curvature of the femur, and the muscles which act on it, serve to reduce the overall level of bending that the bone is subjected to by counteracting the bending moment exerted by the ground reaction

force. This is in contrast to the loading situation in the radius, ulna and tibia, where bone curvature actually promotes greater stress. The latter loading situation has been shown to occur in the radius of the horse as well (Biewener *et al.* 1983).

Because of its lack of curvature, the net orientation of bending in the chipmunk femur is in the cranial, rather than the caudal direction (not shown). As in the ground squirrel, the adductor and hamstring muscles serve to counteract the bending induced by the ground reaction force acting on the femur, so that the overall level of stress due to bending is reduced. However, the bending moment that they exert is not as great as that exerted by the ground force in the opposite direction. As a result, peak stress develops in the cranial cortex. This is the only bone in either species for which this distribution of stress is observed.

Peak stress versus speed

The magnitude of peak (compressive) stress acting in both the fore and hindlimb bones increases in a generally linear fashion with increased speed (Figs 8, 9, respectively). Again, the range of speeds shown for the chipmunk represents only gallops, whereas some trotting speeds were obtained for the ground squirrel. Too few data are available at trotting speeds to allow peak stress at a trot and at a gallop to be compared. The slope of the increase in peak stress with increasing speed is significantly greater ($P < 0.05$) for the distal fore and hindlimb bones of the ground squirrel than for the more proximal, humerus and femur. This is also the case for the forelimb bones of the chipmunk. The slopes for the chipmunk femur and tibia, however, are not significantly different. Table 3 presents the maximum values of stress that were calculated to act in the cortices of each bone for the two species. Peak (compressive) stresses of up to -58 to -86 MN/m² were measured in the distal bones of the fore and hindlimb. The peak stresses calculated to act in the humerus and femur of each species were substantially less (-31 to -42 MN/m²). These stresses were generally determined at the highest speeds observed. The peak galloping speed of the chipmunk (4.4 m/s) was much higher than that measured for the ground squirrel (3.4 m/s). It seems likely that these speeds are close to the top speeds of these animals. Maximum stress is developed in the caudal cortex of each bone, except the chipmunk femur. This is consistent with the net orientation of bending in each of these bones. The lower magnitude of peak stress observed in the femora of both species, moreover, correlates with the fact that they are loaded primarily in compression, rather than bending.

Table 3. *Peak stresses calculated to act in the midshaft cortices of each bone for the two species*

Bone	Peak stress (MN/m ²)	
	Ground squirrel Caudal/Cranial	Chipmunk Caudal/Cranial
Humerus	-3.2/+28.7	-41.2/+33.0
Radius	-75.6/+44.4	-86.3/+65.1
Ulna	-73.3/+55.1	-70.6/+44.7
Femur	-42.0/-13.9	-31.0/-39.2
Tibia	-65.8/+47.2	-57.5/+43.8

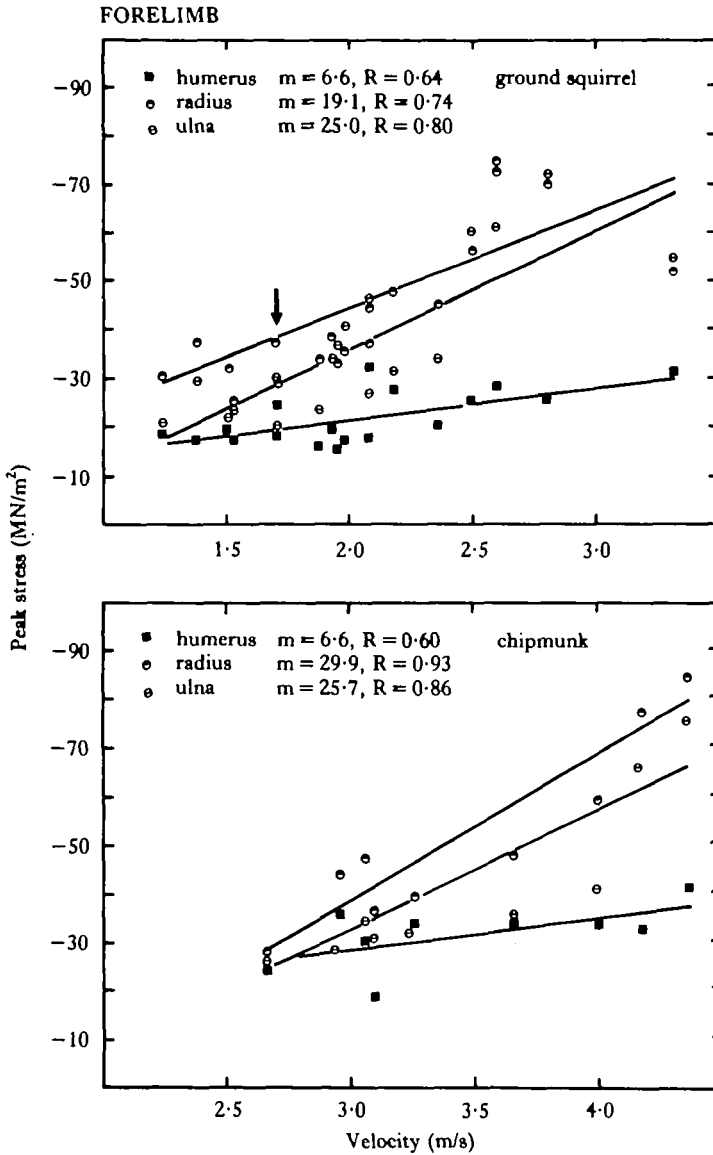


Fig. 8. Peak (compressive) stress plotted against velocity in the forelimb bones of the ground squirrel and chipmunk. The lines were determined from a least squares linear regression of the data. The slopes of the increase in peak stress in the more distal bones, the radius and ulna, are significantly greater than the slope of the humerus for each animal:

		95% confidence interval of	
		the slope	S.E.
ground squirrel	radius	10.8-27.4	9.5
	ulna	15.1-34.4	10.3
	humerus	2.5-10.7	4.3
chipmunk	radius	19.0-40.8	7.8
	ulna	11.9-39.5	9.9
	humerus	-1.3-14.5	5.7

The slope (m) and correlation coefficient (R) for each bone are indicated. Note the different range of speeds for the chipmunks versus the ground squirrels. The arrow indicates the trot-gallop transition speed for the ground squirrels.

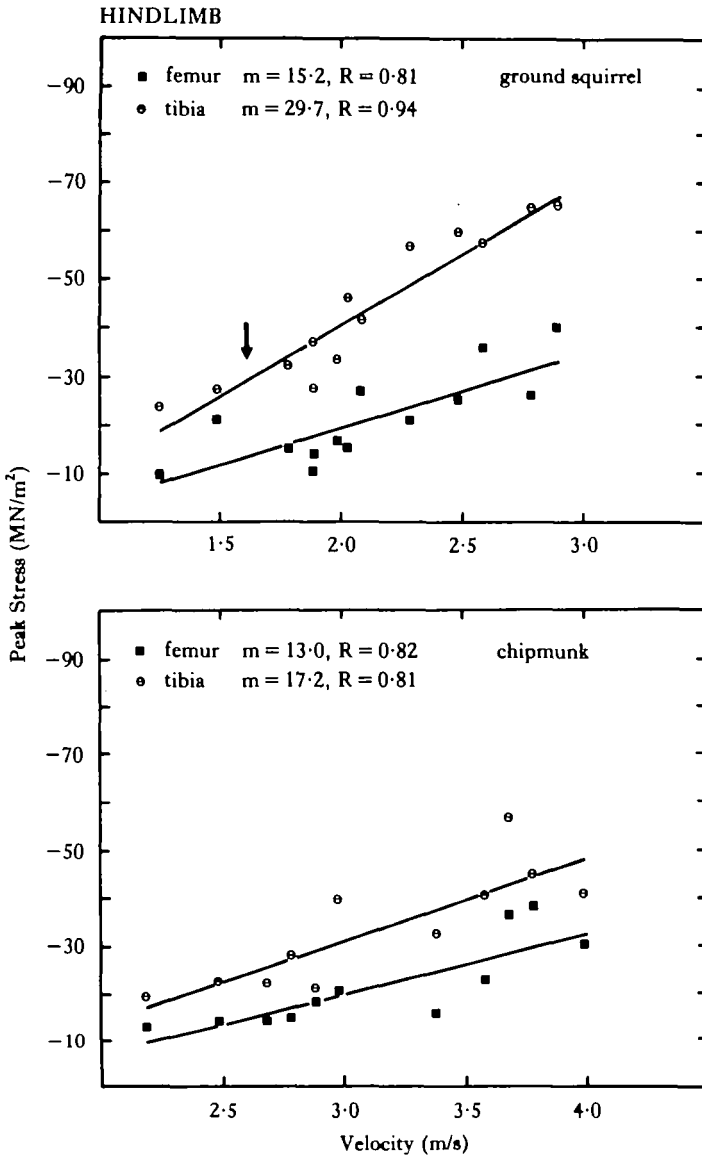


Fig. 9. Peak (compressive) stress plotted against velocity in the hindlimb bones of the ground squirrel and chipmunk. The slope of the increase in peak stress in the tibia of each animal is greater than the slope for the femur. Only in the ground squirrel is the difference significant:

		95 % confidence interval of the slope	S.E.
ground squirrel	tibia	23.1-36.3	5.3
	femur	8.1-22.3	6.0
chipmunk	tibia	8.2-26.2	7.3
	femur	6.3-19.7	5.5

The slope (m) and correlation coefficient (R) for each bone are given. Note the different range of speeds for the chipmunks versus the ground squirrels. The arrow indicates the trot-gallop transition speed for the ground squirrels.

DISCUSSION

The greater level of stress (1.5 to 2 times) developed in the more distal fore and hindlimb bones suggests that safety factors may vary for different bones within an animal's skeleton. The method used in this study to calculate stress assumes, however, that antagonistic muscles remain inactive during the support phase of the limb. With a greater mass of musculature (and fibre cross-sectional area) exerting force on the humerus and femur, if antagonistic muscles were active to stabilize joints or aid in control of movement, then stresses developed in these bones could be significantly greater than those calculated.

The shape and mass of a bone appear to represent selection of adaptive remodelling of the bone to its unique mechanical environment (Lanyon & Bourn, 1979). Hence, the reduced mass (and thus, A and I) of the radius, ulna, and tibia may reflect the need to lower moments of inertia, minimizing the energy expended to accelerate and decelerate the limbs in each stride. Such an energy saving might balance the danger of having a comparatively lower safety factor for these bones. The increased magnitude of stress that the more distally located bones are subjected to in the ground squirrel and chipmunk correlates with data obtained for racehorses, showing that the long bones having the greatest probability of fracture in these animals are those most distal in the limb, the metacarpus and metatarsus (Currey, 1981). Peak stresses measured in the radius of horses during steady state locomotion, however, were found to be significantly greater than those acting in the metacarpus (Biewener *et al.* 1983). This seems to conflict with the data for the probability of fracture in these two bones, and with the present observations in the ground squirrel and chipmunk. But when stresses were measured during events of acceleration and deceleration, they were found to be substantially elevated in the metacarpus and similar in magnitude to those in the radius; bearing out the importance of considering non-steady state events. Smaller animals probably undergo even greater accelerations (and decelerations) than larger animals during locomotion, as well as in climbing and jumping. Stresses developed during such events may be greater than those calculated here and may therefore also have selective and functional significance for the mass and shape of a bone.

Peak stress versus body size

The peak stresses measured in the limb bones of ground squirrels and chipmunks galloping at high speeds (range: -31 to -86 MN/m²), although slightly smaller, are similar in magnitude to those calculated to be acting in the bones of much larger animals operating near their top performance while jumping (dog: -100 MN/m²; Alexander, 1974), hopping (kangaroo: -120 MN/m²; Alexander & Vernon, 1975), and galloping (buffalo: -58 to -113 MN/m²; Alexander, Maloiy *et al.* 1979; horse: -78 to -102 MN/m²; Biewener *et al.* 1983). The measurements of stress in the larger animals were based on a film/force plate analysis similar to the one used in the present study. However, in the study of the locomotory stresses developed in the radius and metacarpus of the horse, Biewener *et al.* (1983) used rosette strain gauges attached these bones to record *in vivo* bone strain simultaneously with records of ground

force and light cine films of limb position. The results of their work show that the film/force technique is susceptible to error in the determination of the transverse component of ground force (R_t) acting on the bone. The larger bending moments calculated to be acting about the midshafts of these bones using the film/force analysis, due to an overestimation of R_t , resulted in the determination of peak stresses that were as much as 1.5 to 2 times greater than those measured from the strain gauge recordings. Because of their small size, however, a strain gauge approach for measurement of stress in the chipmunk and ground squirrel is not feasible. To maintain consistency, the magnitude of peak stresses determined here are compared with the values calculated in the larger animals using a similar method of analysis. However, it is important to bear in mind that detailed knowledge of the loading pattern and stress distribution within a bone is limited using the film/force technique.

Given that peak stresses ranging from -30 to -80 MN/m² in small animals and from -60 to -110 MN/m² in large animals commonly occur during normal activity, and that the fracture strength of cortical bone loaded in bending is about 200–250 MN/m² over this range of size (Biewener, 1982), a fairly uniform safety factor (ratio of fracture stress to peak functional stress) of about two to four appears to have been selected for over a range in size. It might be argued that small animals have a slightly greater safety factor than larger animals, but this cannot be demonstrated clearly because of the error involved in the calculation of stress by this technique. A similar range of safety factors (2–5) has been shown to exist for the bones and tendons of vertebrates studied over a wide range of strenuous activities based on data obtained from different methods of measurement (Alexander, 1981).

This is in disagreement with the scaling prediction that peak stresses should increase with increasing size (Biewener, 1982). This prediction was based on empirical data describing the allometric relationships for length and diameter (Alexander, Jayes *et al.* 1979), as well as area and second moment of area (Biewener, 1982), of various limb bones over a wide range in body size. These data show that the mammalian skeleton scales close to geometric similarity. As a consequence, the geometry of an animal's bones will tend to promote greater stresses as size increases, if we make the single assumption that the forces acting on the bones increase in direct proportion to the animal's body weight. Over a range in size from a 0.09 kg chipmunk to a 300 kg horse, peak stress would be predicted to increase nearly ten-fold. Because functional stresses are of similar magnitude over a range in size, large animals must compensate, then, for the scaling of their skeleton by reducing the forces (F_a and F_t) acting on them.

A decrease in the axial and transverse forces acting on a bone could be achieved in a number of ways. Alexander, Langman & Jayes (1977) have shown that large ungulates have greater duty factors than smaller ungulates running near their top speed, which would allow them to reduce the magnitude of peak ground force acting on their limbs. Force plate data obtained for animals of different sizes indicates that the peak magnitude of ground force decreases slightly (as a multiple of body weight) with increasing size (Cavagna, Heglund & Taylor, 1977). However, the peak magnitude of the vertical component of ground force (F_v) measured for the forelimb of a horse (270 kg) reaches 1.7 times body weight at a gallop (Biewener *et al.* 1983). This is not significantly less than that measured for the ground squirrel forelimb (1.8 times

and chipmunk forelimb (2.4 times). The corresponding values for the hindlimbs of these two species are 1.3 and 1.8 times body weight, respectively. Moreover, McMahon (1977) measured the period of support of the forelimbs as a fraction of stride period, as well as peak vertical acceleration of the centre of mass, at the trot-gallop transition speeds of different sized animals and found no change with body size, which is at variance with the results of Alexander *et al.* (1977). Consequently, it is not clear whether larger animals reduce the forces acting on their bones by increasing the time over which force is exerted on the ground and thus decrease the peak force exerted on the limb.

A decrease in peak stress can most effectively be achieved by simply reducing the level of bending that a bone is subjected to. A relatively small force, acting to load a bone in bending, produces a much larger magnitude of stress than a significantly greater force, acting to load the bone in compression. The importance of this is borne out by the loading observed in the three forelimb bones of the ground squirrel, as well as in its tibia. For example, in the tibia the magnitude of F_t is three times less than F_a at a gallop, yet the magnitude of stress that F_t produces in the bone's cortices at its midshaft is 20 times greater than that due to F_a (neglecting the bending exerted by F_a due to the bone's curvature).

One scheme by which the skeletal morphology of an animal's limb can be altered to lower bending stresses is simply to reduce bone curvature. I have shown that the effect of curvature in the radius, ulna, and tibia of the ground squirrel and chipmunk is to augment the magnitude of bending stress developed in these bones. Because the magnitude of the axial force acting on a bone is much greater than the transverse force, even a small degree of curvature induces a bending moment that can be significantly greater than that due to the transverse force. If the objective of bone remodelling or a bone's shape is to minimize the magnitude of bending stress (Pauwels, 1968; Frost, 1964, 1979) or peak stress, in general, then the adaptive advantage of bone curvature is not clear. Lanyon (1980) has shown that the longitudinal curvature of the rat tibia develops in response to the functional loads applied to it during normal use, rather than its inherited genetic programme, and argued that bone curvature may develop to provide adequate space for packaging of muscles around the bone, or to maintain a stress 'threshold' necessary for healthy bone tissue. Neither of these possibilities has been demonstrated. In fact by reducing longitudinal curvature as well as the bone's mass, the hypothesized 'threshold' of stress could still be achieved, with the added advantage of lowered limb weight. The situation however is more complicated than this. The curvature of the ground squirrel femur is orientated so that the bending induced by it acts to counteract, rather than augment, the bending exerted by the transverse force on the bone. As a result, the overall level of bending is reduced. In general, though, it appears that bone curvature promotes, rather than reduces, peak stresses acting in a bone. Hence, if bone curvature decreases in a general way with increasing body size, this could represent an important means by which large animals reduce peak stress.

A second way that bending stresses can be lowered is by reducing the magnitude of the net transverse component of the ground force acting on a bone. The transverse component of the ground force can be decreased by aligning the limb (or bone) more closely in the direction of the vector of ground force, maximizing its axial component

of force. This is observed in the loading of the radius and ulna of the forearm of both the ground squirrel and chipmunk. These bones are relatively slender in each animal. The magnitude of bending that they are subjected to is kept low by maintaining a close alignment to the direction of the ground force throughout the support phase (Fig. 3A). If these bones were loaded even 15° off their axes, stresses as great as -185 (radius) to -230 (ulna) MN/m^2 would be developed at high speeds, and they would probably fracture. Bending can also be reduced by having muscles more closely aligned with the longitudinal axis of a bone. The arrangement of the muscles in the fore and hindlimbs of both species seems to conform in a general way with this scheme (Table 2). Only in the case of the femur do the adductor and hamstring muscles act at a significant angle to the longitudinal axis of the bone (the medial and lateral heads of the triceps act at a large angle to the humerus, but the force they can exert is small). However, the orientation of these muscles actually serves to counteract the bending moment exerted by the transverse component of the ground force on the femur, rather than to increase it.

The magnitude of peak stress incurred during the locomotory activity of an animal not surprisingly represents an important factor in the design of skeletons over a range in size. How frequently 'peak' stresses are applied during the normal activity of different animals and what effect frequency (as well as magnitude) has on the remodelling response of a bone within an animal's lifetime, or on selection for a given shape and muscular organization over many generations, is not known. Clearly large size places restrictions on an animal's locomotory ability. But within the context of steady state, terrestrial locomotion, measurements of peak stress in two species of small mammals compared with those in larger mammals demonstrates that a fairly uniform safety margin to failure is maintained. To accomplish this, larger animals must reduce the forces and, more importantly, the bending moments exerted on their bones (proportional to body weight) compared to small animals. The factors which are important in governing this seem to be bone curvature, the organization and orientation of muscles acting on a bone, and the orientation of the limb itself. However, the relative importance of these factors is complicated by their interaction with one another.

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GLOSSARY OF TERMS USED IN THE TEXT AND FIGURES

- A cross-sectional area, mm^2
- I second moment of area of bone's midshaft, mm^4
- c maximum distance from the neutral plane of bending to the surface of the bone's cortex, mm
- L distance to the midshaft of a bone from its distal end, mm

- moment arm of axial forces exerted at bone's midshaft due to curvature along its length, mm
- x moment arm of muscle(s) acting about a joint, mm
- α angle of muscle to the bone's longitudinal axis, degrees
- F_v vertical component of ground reaction force, N
- F_h horizontal component of ground reaction force, N
- R resultant ground force acting on a bone, N
- R_a axial component of ground force acting on a bone, N
- R_t transverse component of ground force acting on a bone, N
- P force exerted by muscle(s) on a bone, 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
- α_c compressive component of stress, MN/m²
- α_b bending component of stress, MN/m²
- α_{cr} stress in the cranial cortex, MN/m²
- α_{cd} stress in the caudal cortex, MN/m²
- M_a moment exerted by the ground force about the ankle

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