

BONE STRAIN: A DETERMINANT OF GAIT AND SPEED?

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SUMMARY

Principal strains were recorded *in vivo* from the radial and tibial midshafts of three goats as they increased speed and changed gait. These data were compared with strain data measured for the radius and tibia of the dog (Rubin & Lanyon, 1982) and the horse (Biewener, Thomason & Lanyon, 1983*b*) in order to test the hypothesis that similar peak bone strains (stresses) occur at functionally equivalent points in the gaits of different species. Multiple recordings of *in vivo* strain along the caudal diaphyses of the radius and tibia of one goat were made to test the validity of this technique for measuring peak locomotor stress. Measured strains were extremely consistent over the animal's full range of speed (coefficient of variation for the radius 0.05–0.08, and for the tibia 0.06–0.11). The data from the three gauges, which were spaced 15 mm apart, demonstrated that maximal strains act at the midshaft, substantiating the use of this technique to measure peak locomotor bone strains. Strain levels recorded at the trot–gallop transition and top galloping speeds of the goat were similar to the values reported for the dog and horse, despite large differences in absolute speed (goat, 4.3 ms⁻¹; dog, 6.9 ms⁻¹; horse, 7.5 ms⁻¹ at maximum gallop). The second moments of area of the tibia and radius (+ ulna) of the dog are 29 % and 113 % greater than for goats of equal size, explaining how similar strains are achieved in the dog at higher speeds than the goat. Furthermore, peak bone strains recorded at the fastest trotting speed were similar to those recorded at the fastest galloping speed for each species. Peak strains recorded for the goat at a maximum gallop correspond to stresses of +37.9 MPa (cranial) and –47.7 MPa (caudal) in the radius and +36.3 MPa (cranial) and –50.3 MPa (caudal) in the tibia, representing a safety factor to yield failure of three.

INTRODUCTION

It seems reasonable to expect that peak stresses (in bone, muscle and tendon) developed near the limits of normal locomotor performance may represent an important determinant of structural design. Previous studies have shown that peak skeletal stresses developed during strenuous locomotor activity are quite similar in mammals over a range of more than four orders of magnitude in body mass

Key words: bone strain, bone geometry, gait, speed.

(Alexander, 1974; Alexander & Vernon, 1975; Biewener, 1983*a*; Biewener *et al.* 1983*b*; Rubin & Lanyon, 1982, 1984). This result is not surprising given that the bones of these animals have similar material properties or strength characteristics (Biewener, 1982; Currey, 1970; Reilly & Burstein, 1975). Therefore, in general, similar safety factors to failure are achieved.

However, no studies have compared peak stresses developed at equivalent points of gait between species of different size, nor have any studies dealt with variation in skeletal design, skeletal loading and locomotor performance between animals of similar size. For instance, ground squirrels and rats, or horses and cows, clearly differ in their locomotor abilities. In particular, cursors achieve greater speed ranges within gaits and much higher top speeds than non-cursors of similar body mass (unpublished data from our laboratory). It seems reasonable to expect that peak skeletal stresses in these animals, both within and between size classes, are similar at their respective gait transitions and top speeds. To test this idea, we have measured *in vivo* bone strains from the radial and tibial midshafts of goats and compared these values to published values for dogs (Rubin & Lanyon, 1982) and horses (Biewener *et al.* 1983*b*; Rubin & Lanyon, 1982). All three species exhibit a number of cursorial specializations (Hildebrand, 1974), but dogs and horses are specialized for high-speed locomotion over level terrain and can achieve 60–100 % greater top speeds than the goat.

We also evaluated the reliability of the technique by making multiple strain recordings along the radial and tibial diaphyses of one goat to determine the variation in strain recorded locally at the midshaft region. This allowed us to determine for the first time how well strain gauge data represent whole bone loading, and how much positional variation in measured strain could be expected when comparing strains at functionally equivalent sites on the bones of different species.

MATERIALS AND METHODS

Animals

Three adults goats (body mass: 25, 26 and 30 kg) were trained to run on a motor-driven treadmill. The animals were considered 'trained' when they ran evenly and changed gait smoothly at a consistent tread speed. The training period generally lasted 2 weeks for each animal. The animals were housed outdoors in a pasture throughout the experiments. Ground reaction forces were measured for limbs over a range of speeds prior to surgery using a Kistler force plate (model 9261A). Rosette strain gauges were attached to the cranial-midshaft (CRM) and caudal-midshaft (CAM) cortices of the right radius of the forelimb and the right tibia of the hindlimb under general anaesthesia (halothane). The operative procedure was similar to that previously described (Biewener *et al.* 1983*b*; Lanyon, 1976). The rosette gauges were soldered to 32 AWG etched-Teflon leads. The lead wires were insulated with separate coats of polyurethane, acrylic and polysulphide epoxy (M-coat series; Micro-Measurements). The gauges were attached with a self-catalysing cyanoacrylate adhesive, following removal of the periosteum, light scraping, defatting and

drying of the bone's surface. The animals were allowed 2–3 days recovery. *In vivo* strains were then recorded each day over a 5- to 7-day period. Ground reaction forces were also recorded and compared to pre-operative measurements to assess lameness caused by attachment of the gauges. Postoperative ground force records for the forelimb were 9–14% lower than those recorded before surgery, while weight support on the hindlimb was 18–24% lower than normal. Consequently, our measurements probably underestimate the magnitude of peak strain (or stress) in normal animals by about these percentages.

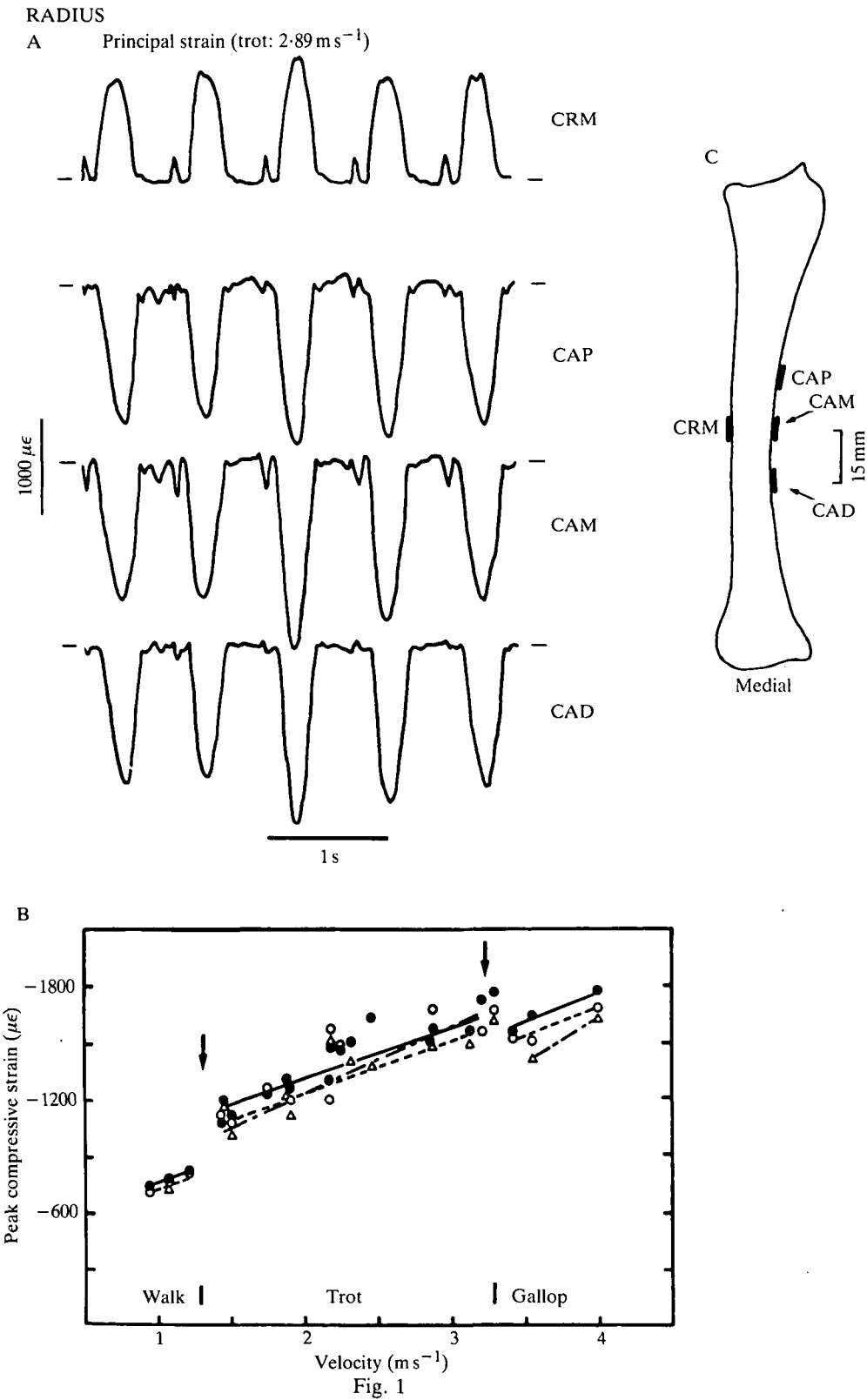
Strain data were collected while the animal moved at a constant speed on the treadmill over a range of speeds and gaits. Zero level strains were taken to be at the plateau point during the swing phase of the limb (e.g. see Figs 1, 2), as has been the convention adopted in previous studies (Biewener *et al.* 1983b; Carter *et al.* 1980; Lanyon & Bourn, 1979; Rubin & Lanyon, 1982). These levels were consistent with the strain levels recorded when the animal's limb was held off the ground in a relaxed state. This was done immediately before each recording session when the bridge circuits were balanced. Gauge orientation to the bone's longitudinal axis was determined from A/P radiographs of the bone. The animals were killed following completion of the strain recordings and their tibiae and radii removed for calculation of geometric properties.

Data analysis

The raw strain data were sampled *via* an A/D converter (sampling rates ranged from 100 to 300 Hz depending on the animal's velocity) and entered into a micro-computer. Principal strains and their orientation to the bone's longitudinal axis (φ) were determined using standard engineering formulae (Dally & Riley, 1978). The larger principal strains (regardless of sign) are discussed here, as these are most relevant to forces exerted on the bone during locomotion and to which bone shape is most critical (see Biewener *et al.* 1983b; Rubin & Lanyon, 1982, for discussion). A minimum of five sequential strides was sampled at each speed. Data are presented as the mean \pm S.D. The coefficient of variation (CV) of peak strain for a series of strides at a given speed was typically less than 0.07. Student's *t*-test for unpaired observations of groups of different size and unequal variances (for the goat–dog and horse–dog comparisons) were conducted to establish significance levels (Sokal & Rohlf, 1969). Least-squares linear regressions were carried out and 95% confidence limits established for peak strain data *versus* running speed within a species, to evaluate and compare the magnitude of strain at specific points of gait.

Validation of the technique using multiple strain recordings

As direct measurement of bone strain is limited to the site at which the gauges are attached, the bone strain technique we have used is susceptible to any variation in local strain concentrations due to, for example, inhomogeneity of material properties or muscles acting nearby on the bone. To assess the magnitude of this variation in strain along the length of the bone, we attached three rosette gauges linearly along the caudal aspect of the radial and tibial diaphyses of one goat (C) (Figs 1, 2). The



gauges were spaced approximately 15 mm apart, with the central gauge of the radius and proximal gauge of the tibia located at the midshaft. Because the cranial aspects of both bones are free of muscle insertions, and assuming that bone tissue inhomogeneity has a negligible effect on surface bone strains, only one gauge was attached to the cranial aspect of each bone.

In vivo principal strains recorded at multiple sites along the caudal (posterior) cortex of the radius (Fig. 1A) and the tibia (Fig. 2A) of goat C were markedly consistent in the magnitude, pattern and sign (tension *versus* compression) of strain. This consistency was found over the full range of speed and gait studied (Figs 1B, 2B). Over the range of trotting speeds, regression slopes of peak strain at each of the sites on the radius were not significantly different from one another (Table 1). While strains recorded from the CAM and CAD1 sites on the tibia were similar, strains recorded at the CAD2 site, compared to the CAM site, were significantly lower. Due to the distal shift in alignment of the tibial recording sites (with a reduction in the bending moment at this level), this result is not surprising. The coefficient of variation for peak principal strain at each speed between these sites ranged from 0.05 to 0.08 for the radius and 0.06 to 0.11 for the tibia. Further, maximum strains were nearly always recorded at the midshaft sites of each bone, as has been previously argued (Biewener *et al.* 1983*b*).

In addition to strain magnitude, the orientation of maximum principal strain (to the bone's longitudinal axis, φ) recorded among the different sites was similar for both bones over the entire speed range of the animal (Table 2). φ was most consistent in the caudal recording sites on the radius. This regular distribution and pattern of locomotor strains, and their orientations, within a stride and over a range of gait, have been noted for several other species (Biewener *et al.* 1983*b*; Lanyon, 1981; Lanyon & Bourn, 1979; Rubin & Lanyon, 1982). Based on these data, the influence of localized stress concentration due to muscular forces or non-uniformity in the underlying bone structure and its properties was considered to be negligible.

RESULTS

Bone geometry

Consistent with the greater absolute speed achieved by the dog at a trot and at a gallop (and the presumably increased loading on its limbs) compared to the goat, the midshaft cross-sectional area and second moment of area of the dog tibia are 19 % and 29 % greater than the values for the goat tibia (normalized for differences in body

Fig. 1. (A) Representative recordings of the maximum principal strains at the different sites shown in (C) for the radius of goat C at a trot of 2.89 m s^{-1} . Five sequential strides are shown. The scale bars indicate strain magnitude and time. The tick marks indicate zero strain. (B) A graph of peak compressive strain (mean values for \geq six strides at each speed) plotted *versus* velocity for each of the caudal gauges. Note that compressive strains are defined as negative. Regression lines for strain data over the range of trotting speeds are shown. These are not significantly different from one another (see Table 1 for statistics). The arrows indicate the walk-trot and trot-gallop transitions (CAP, caudal proximal, \bigcirc -....; CAM, caudal-midshaft, \bullet —; CAD, caudal distal, \blacktriangle ---). (C) Medial view of the right radius. CRM, cranial midshaft.

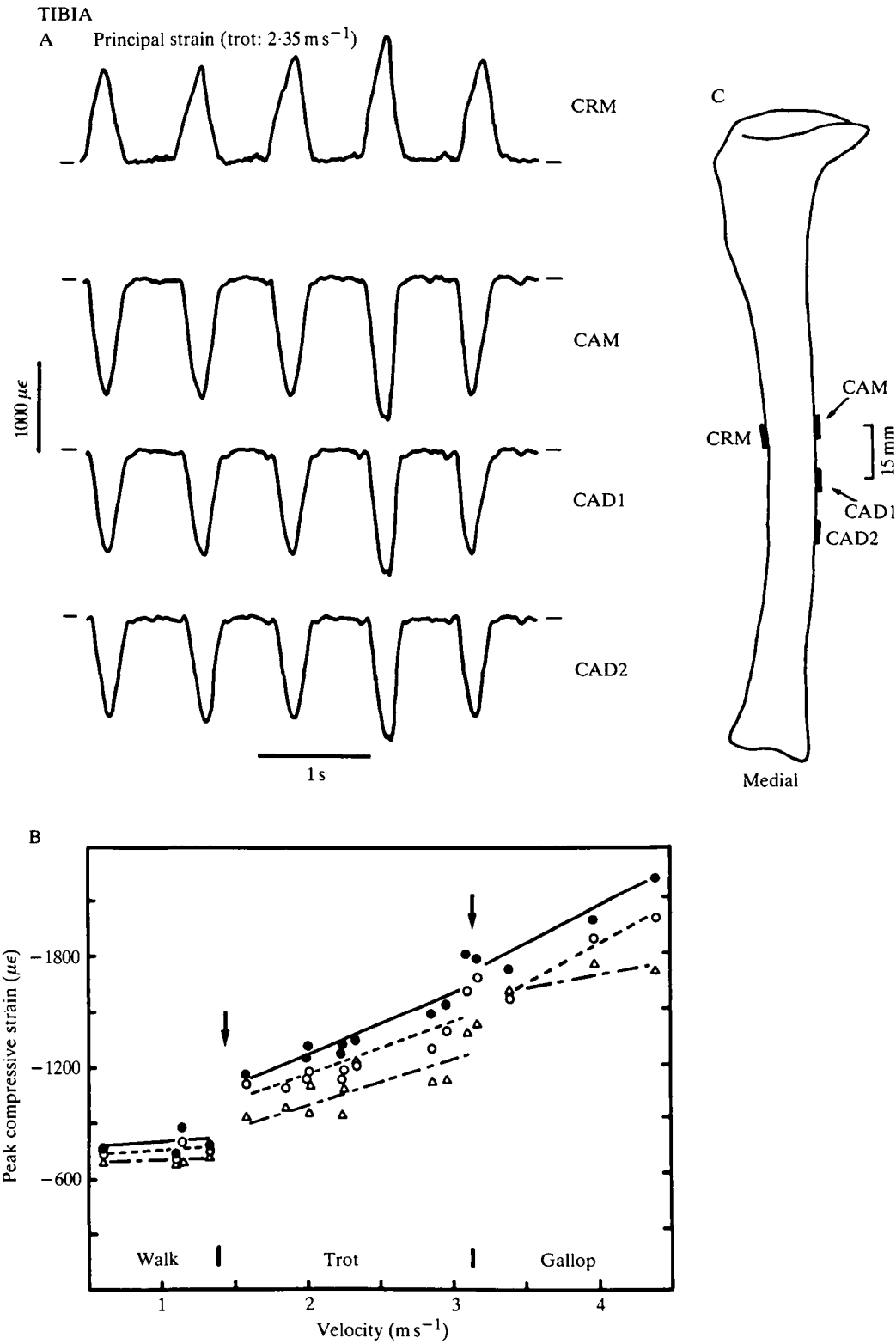


Fig. 2

Table 1. *Least-squares linear regression statistics for in vivo principal strain data versus running speed (independent variable), conforming to the form $y = bx + a$*

Dependent variable		b ($\pm 95\%$ CI)	a	r	N
Multiple strain recordings at the trot					
Radius	CAP	-284 (201)*	-661	0.78	9
	CAM	-278 (76)*	-766	0.90	16
	CAD	-357 (232)*	-587	0.81	9
Tibia	CAM	-346 (134)*	-568	0.92	9
	CAD1	-285 (132)*	-570	0.89	9
	CAD2	-211 (205)*	-587	0.67	9
Peak CAM strain					
Radius	Trot	-285 (195)*	-728	0.67	38
	Gallop	-35 (358)	-1496	0.05	19
Tibia	Trot	-378 (75)*	-573	0.86	28
	Gallop	-430 (101)*	38	0.95	12
Peak CRM strain					
Radius	Trot	336 (137)*	361	0.73	25
	Gallop	312 (313)	217	0.55	13
Tibia	Trot	212 (129)*	573	0.64	23
	Gallop	438 (256)*	433	0.84	13
Bending: compressive strain					
Radius	All gaits	-0.08 (1.18)	7.94	0.03	34
Tibia	All gaits	-0.42 (1.70)	12.60	0.09	32

Equations are for all three goats, except those for multiple strain recordings at different sites on the radius and tibia of goat C (CRM, cranial-midshaft; CAP, caudal-proximal; CAM, caudal-midshaft; CAD, caudal-distal).

* Denotes slope is statistically significant ($P < 0.05$).

mass; Table 3; Fig. 3). Because of its small size, we have ignored the dog fibula in this comparison (goats lack a fibula). Whether or not the fibula bears significant load in relation to its size ($<10\%$ of tibial cross-sectional area) is unknown, but it can only increase the cross-sectional area and effective second moment of area of bone resisting loads transmitted between the ankle and knee of the dog.

In contrast to the tibia, the midshaft cross-sectional area and second moment of area of the dog radius are 35% and 51% less than the values for the goat. This is due, however, to differences in the size of the ulnae of these two species (Fig. 3). In goats, and ungulates in general, the ulna is greatly reduced. At the midshaft level of the radius where we recorded bone strain, the shaft of the ulna is nearly lost, accounting for less than 11% of the total cortical cross-sectional area of the two forearm bones combined. In contrast, the ulna of dogs is retained as a major supportive element between the carpus and elbow, representing 42% of the total cortical cross-sectional

Fig. 2. (A) As in Fig. 1, representative recordings of the maximum principal strains at the different sites shown in (C) for the tibia of goat C at a trot of 2.35 m s^{-1} . (B) Graph of peak compressive strain plotted *versus* velocity for each of the caudal gauges, with regression lines for the range of trotting values shown. As in the radius, the slopes of these lines are not significantly different from each other, though predicted values of strain are significantly lower for the CAD2 *versus* CAM site (CAM: \bullet —; CAD1: \circ -----; CAD2: \triangle ---). (C) Medial aspect of right tibia. Abbreviations as in Fig. 1.

Table 2. *Orientation* of the maximum principal strains (E1) to the bone's longitudinal axis (φ ,°) recorded at the different sites on the radius and tibia of goat C*

Gait	Radius			
	CAP	CAM	CAD	CRM
Walk	-5 ± 3 (10)	-10 ± 2 (20)	-8 ± 3 (20)	$+8 \pm 3$ (20)
Slow trot	-3 ± 2 (27)	-14 ± 4 (36)	-9 ± 3 (26)	$+2 \pm 5$ (26)
Fast trot	-11 ± 4 (32)	-13 ± 3 (32)	-14 ± 3 (23)	-2 ± 6 (24)
Gallop	-17 ± 4 (14)	-14 ± 3 (39)	-17 ± 4 (18)	-2 ± 5 (23)

	Tibia			
	CAM	CAD1	CAD2	CRM
Walk	-5 ± 2 (31)	-24 ± 2 (22)	-9 ± 4 (20)	-17 ± 3 (21)
Slow trot	0 ± 6 (33)	-25 ± 4 (33)	-8 ± 5 (22)	-20 ± 2 (22)
Fast trot	-3 ± 6 (40)	-22 ± 2 (39)	-9 ± 3 (27)	-17 ± 2 (26)
Gallop	-5 ± 3 (38)	-21 ± 2 (23)	-8 ± 2 (25)	-12 ± 3 (35)

* $\varphi < 0^\circ$: proximal-lateral; $\varphi > 0^\circ$: proximo-medial.

Values are the mean \pm S.D. for two to four runs at each gait range (*N* is given in parentheses).

Although individual variation in φ was found at equivalent bone recording sites (typically $< 15^\circ$), as with goat C, φ remained consistent in goats A and B at each site over each animal's full range of speed.

Table 3. *Mean bone geometric data for goats and dogs*; where A and I are the area and second moment of area, respectively, measured at the bone's midshaft, and L is the bone's length*

Animal	Mass (kg)	Tibia			Radius			(Radius + ulna)	
		A (mm ²)	I (mm ⁴)	L (mm)	A (mm ²)	I (mm ⁴)	L (mm)	A (mm ²)	I (mm ⁴)
Goat (\pm S.D.)	27	91 (15)	1118 (212)	191 (13)	111 (7)	940 (214)	133 (12)	122	946
Dog	36	127 (5)	2000 (213)	195 (7)	86 (4)	643 (18)	178 (6)	154	3036
Dog scaled†	27	108	1438		73	462		125	2012

* Unpublished data for two dogs from our laboratory.

† Values calculated for dog scaled to 27 kg body mass assume scaling exponents ($A \propto M^{0.72}$ and $I \propto M^{1.43}$) given by Biewener, 1982.

Values are also presented for the radius in combination with the ulna, as loads transmitted through the forearm are distributed between these two bones. The dog fibula is ignored in the comparison of the hindlimb (goats lack a fibula) because of its extremely small size.

Standard deviations are given in parentheses.

The goat ulna is reduced and much smaller than the dog ulna at the level of the radial midshaft, explaining the similar magnitude of strains developed in the bones of the two species, despite much higher speeds achieved by the dog.

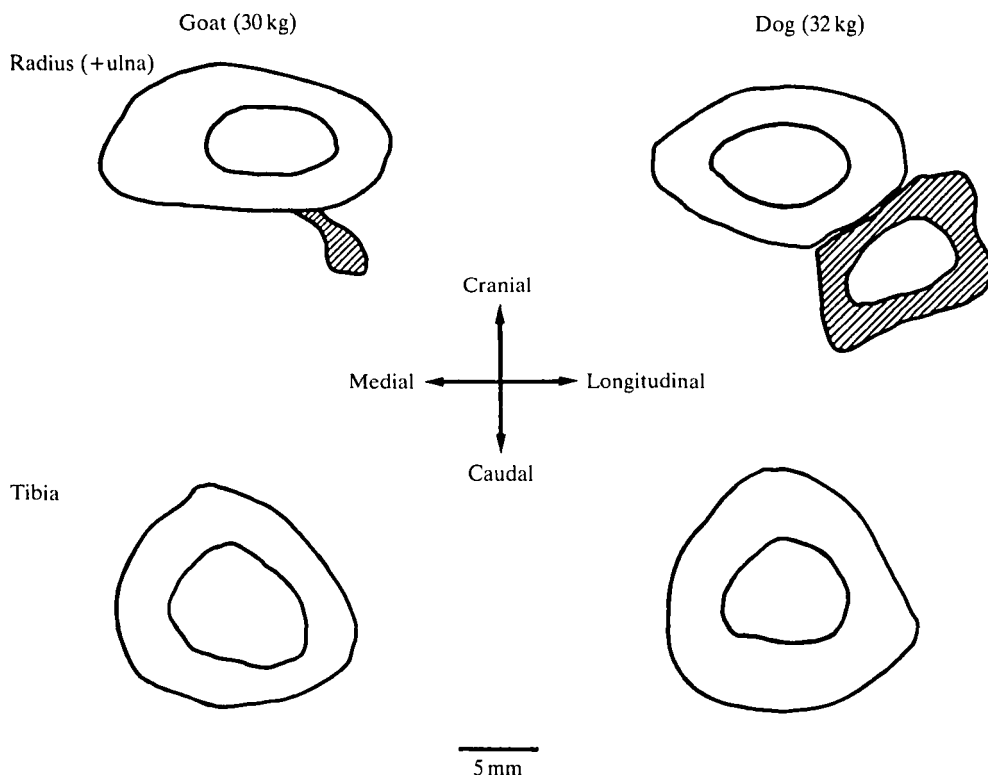


Fig. 3. Drawings of the cross-sectional geometry of the radius (and ulna, shaded) and tibia of (A) a goat and (B) a dog at the level of their midshafts. The ulna of the dog is significantly larger than that of the goat and provides increased resistance to bending forces acting on these two forearm bones (see Table 3 for geometric data). The comparatively larger size of these bones in the dog correlates with the greater speeds that the dog achieves, while sustaining peak strains similar to those acting in the bones of the goat.

area of the two forearm bones combined (61.8 mm^2 , mean value for the ulnae of two dogs). The second moment of area for the dog radius and ulna combined (which measures the effective resistance to bending loads transmitted through the forearm), moreover, is much greater than that for the radius alone (Table 3). The total cortical cross-sectional area and second moment of area of the two forearm bones of the dog (scaled to the mean body mass of the goats) are 3 % and 113 % greater than in the goat, when we account for the additional load borne by ulnae of each species.

Bone strain versus gait

Trot-gallop transition

The transition from a fast trot to a gallop may be expected to redistribute the forces acting on the limb to reduce peak bone strain, enabling a further increase in speed at a gallop, before a level of peak strain is again reached similar to that at a fast trot. Consistent with such a redistribution of force, peak strains in the cranial (tensile) and caudal (compressive) midshaft cortices of both bones fell as the animals changed gait

from a fast trot to a slow gallop. This difference was significant at the cranial-midshaft of each bone (16 %) and the caudal-midshaft of the tibia (11 %), but not the caudal-midshaft of the radius (7 %). These comparisons are based on the average strain values (\pm S.E.) at 3.3 m s^{-1} , calculated from the regression equations (Table 1) for the three goats pooled. This is depicted by the overlap in the 95 % confidence intervals of the trot and gallop regressions for the caudal midshaft strains, and the lack of overlap for the cranial midshaft (Fig. 4). Decreases in peak radial and tibial strain amplitude at the trot-gallop transition within individuals, although in certain instances not significant, generally matched the patterns shown for the pooled regressions. The peak radial and tibial strain values at a gallop are for the non-lead limb, as none of the goat used the experimental limb as the lead limb (preferring a left-leg lead, transverse gallop instead). Otherwise, increases in strain were generally linear within a gait (trot and gallop), and rose sharply (40 %) at the walk-trot transition.

Fast trot versus fast gallop

Given that locomotor bone strain represents an important determinant of skeletal design, peak strain may be a limiting factor in determining the maximum speed an animal achieves at a trot and at a gallop. Peak principal compressive (caudal) and peak principal tensile (cranial) strains recorded at the radial (Fig. 4A) and tibial (Fig. 4B) midshafts of the goat support this view. Peak caudal midshaft (CAM) strains for each bone at the animals' top trotting speeds, although lower, were not significantly less than those at their fastest galloping speeds (Table 4). Peak CAM radial strain at a maximal trot ($-1748 \mu\epsilon$) was only 5 % less than that at a maximal gallop ($-1847 \mu\epsilon$; $P > 0.05$), while peak CAM strain in the tibia at a maximal trotting speed ($-1796 \mu\epsilon$) was 9 % less than that at the fastest galloping speed ($-1968 \mu\epsilon$; $P > 0.05$). Similarly, peak tensile strains developed in the cranial midshaft (CRM) of each bone at maximal trotting and galloping speeds were not significantly different ($< 3\%$). The maximum strains recorded at a gallop (Table 4) correspond to stresses of $+37.9 \text{ MPa}$ (CRM) and -47.7 MPa (CAM) for the radius and $+36.3 \text{ MPa}$ (CRM) and -50.3 MPa (CAM) for the tibia, based on a value of 22.5 GPa for the elastic modulus of mammalian bone (mean for the values published by Carter, Harris, Vasu & Caler, 1981; Lipson & Katz, 1984; Schryver, 1978) ($1 \text{ MPa} = 1 \text{ MN m}^{-2}$).

Distribution of bone loading

In both bones, bending predominated, acting to place the caudal cortex in compression and the cranial cortex in tension. The ratio of strain due to bending *versus* axial compression ($\epsilon_b:\epsilon_c$), pooled for all three animals and over their full range of gait, was $8.1(\pm 3.8)$ for the radius and $11.6(\pm 5.1)$ for the tibia. No significant change in the distribution of strain was found throughout the three gaits (Fig. 5), though variation in the relative degree of bending *versus* axial compression existed between individuals. Consistent with the maintained distribution of bending

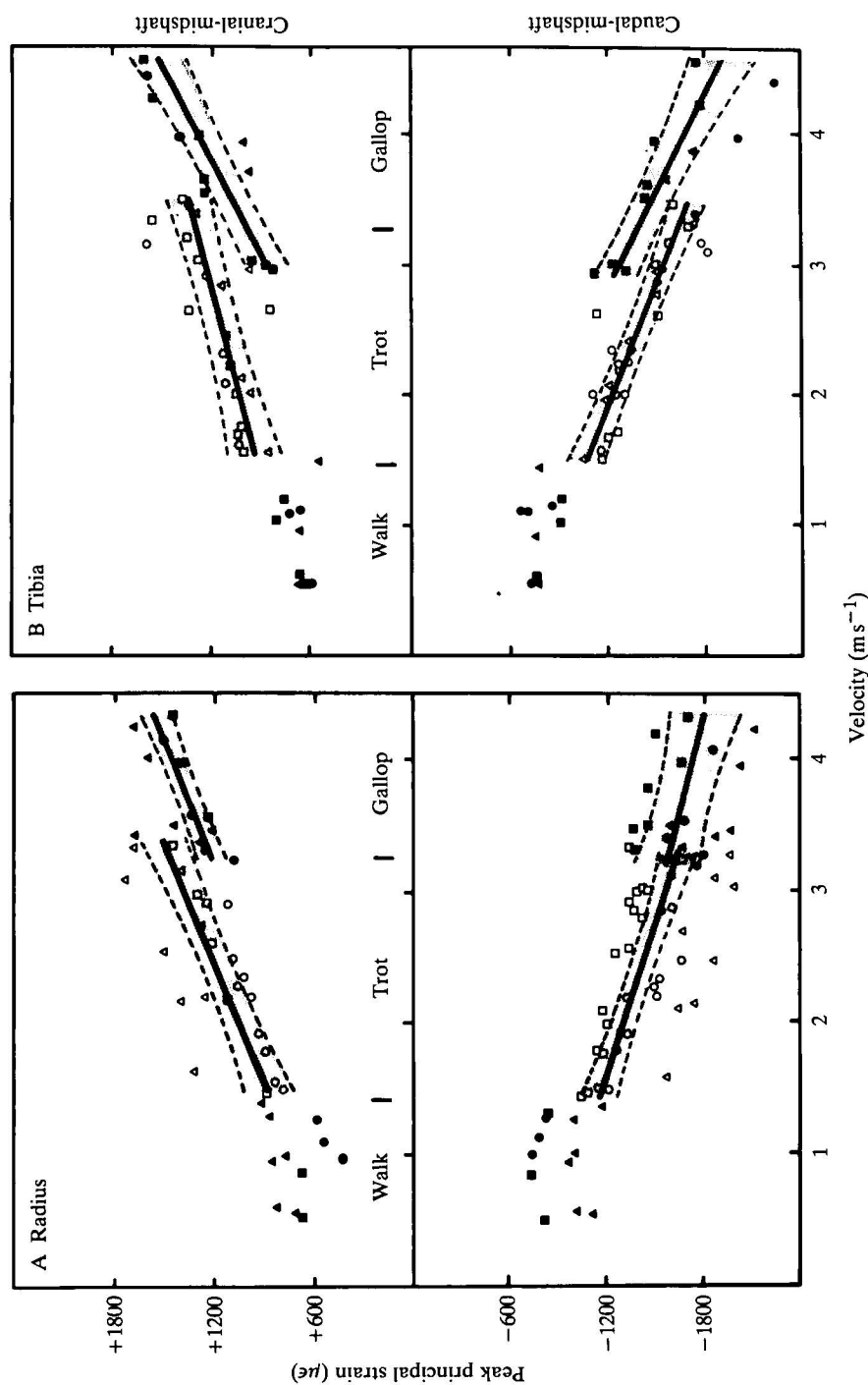


Fig. 4. Graphs of peak principal strain (ϵ_1) plotted *versus* velocity for the cranial (tensile strains) and the caudal (compressive strains) cortices of (A) the radius and (B) the tibia. The values plotted represent the means for a series of strides (≥ 6) at each speed for all three goats in the study. The filled symbols indicate strains at walking and galloping speeds; the open symbols are for trotting speeds. Regression lines are shown for values measured over the ranges of trotting and galloping speeds. The 95% confidence intervals for the regressions are also given (dashed lines and shaded).

Table 4. *Peak principal compressive strains (caudal-midshaft)† versus gait for the radius and tibia of goats (N ≥ 20) compared to dogs (N ≥ 6) and horses (N ≥ 20)*

Gait	Velocity (ms ⁻¹)			Radius			Tibia		
	Goat	Dog	Horse	Goat	Dog	Horse	Goat	Dog	Horse
Walk minimum	0.5	0.7	1.1	-822 (101)	NA	NA	-725 (53)	-702 (35)	-939 (36)*
Walk maximum (Transition)	1.3	1.6	1.8	-832 (82)	-1503 (63)	-1247 (264)	-845 (79)	-1059 (49)	-998 (41)
Trot minimum				-1298 (248)	-1800 (22)	-1791 (198)	-1138 (126)	-1580 (37)	-1255 (85)
Trot maximum (Transition)	3.3	3.6	4.7	-1748 (244)	-2384 (49)	-2049 (187)	-1796 (217)	-2006 (63)	-1743 (151)
Gallop minimum (non-lead)				-1582 (209)	-2087 (22)	-2011 (258)	-1616 (224)	NA	-2363 (226)
Gallop maximum	4.3	6.9	7.5	-1847 (354)	-2248 (41)	-2007 (139)*	-1968 (348)	-2016 (99)	-3140 (76)**

* $N = 6$; ** $N = 12$.

† Goat values are the pooled means for three individuals; dog values are for one individual (Rubin & Lanyon, 1982); horse values are for three individuals pooled (Biewener, Thomason & Lanyon, 1983b), except those at a minimum walk (one) and maximum gallop (two, Rubin & Lanyon, 1982).

Strains are in microstrain ($\times 10^{-6}$).

Standard deviations are given in parentheses.

to compressive load borne by each bone, the orientation of principal strain did not vary significantly over the animals' full range of speed. Principal strain angles (φ) *versus* gait are given in Table 2 for goat C. While individual differences in φ existed at equivalent recording sites, the consistency of strain angle observed for goat C was also characteristic of the other two goats over their full ranges of speed. The strain angle data also reflect the extremely small variability in strain orientation for a series of strides at any given speed. This angle was maintained (less than $\pm 5^\circ$) throughout the support period of the limb.

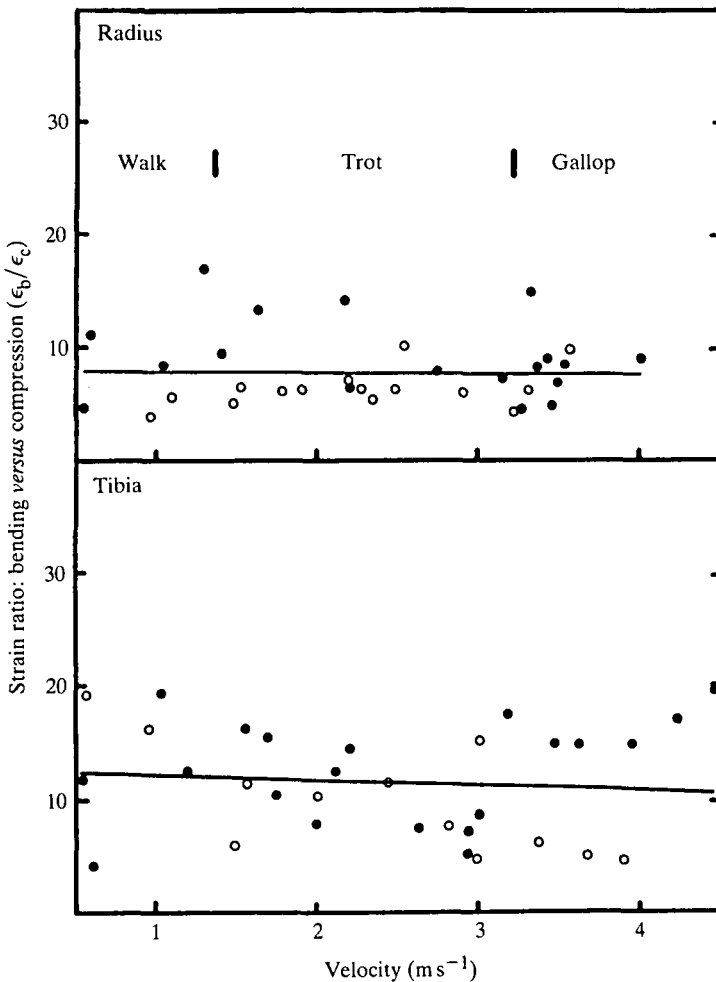


Fig. 5. Graphs of the ratio of strain due to bending (ϵ_b) *versus* axial compression (ϵ_c) at the caudal-midshaft (CAM) of (A) the radius and (B) the tibia of the goat. Values are for two individuals in each case over their full range of speed. The slopes of the regression lines for each bone are not significantly different from zero (see Table 1 for statistics). However, the tibia of goat B (○) exhibited a significant decrease in $\epsilon_b : \epsilon_c$ with increasing speed (-4.13 ± 1.88 , 95 % confidence interval) obscured by the pooled regressions.

DISCUSSION

Validation of the in vivo bone strain technique

The multiple recordings of principal strain along the caudal cortices of the goat radius and tibia provide evidence that the use of rosette strain gauges is a reliable method for determining peak strains developed within a bone. However, as was noted above, this is only true when a site on the bone can be exposed free of nearby muscle insertions. *In vivo* strains recorded at more proximal or distal sites on a bone, near where joint ligaments and muscles attach, may still be susceptible to local distortions in the strain field that are unrepresentative of whole bone loading. These data also support the contention that peak strains occur at the midshaft of a long bone and are representative of the stress developed in response to forces transmitted through the whole of the bone (Biewener *et al.* 1983b).

Skeletal geometry and locomotor performance

For species of similar size, cursorial species may be expected to risk an increased probability of structural damage or failure (lower safety factor) associated with greater peak stresses at higher absolute speeds within a gait, or possess proportionately greater bone mass to maintain a comparable safety factor to failure (i.e. similar peak strains) than less active species (Alexander, 1981). The greater size of the radius (+ ulna) and tibia of the dog compared to the goat suggests that peak locomotor strains are similar in the two species, despite the much greater speeds achieved by the dog at a trot and at a gallop. The much greater second moments of area for the limb bones of the dog (radius + ulna: 113 % and tibia: 29 %) compared to the goat are particularly significant, as these bones are primarily subjected to bending loads (see discussion below). Given the facility of bones to remodel in response to changes in mechanical loading (e.g. Goodship, Lanyon & McFie, 1979; Lanyon & Bourn, 1979; Lanyon, 1981), selection for increased bone mass in the dog is not surprising. However, over a range of body mass the scaling of bone geometry does not account for the similar stresses that have been measured (Alexander, Jayes, Maloiy & Wathuta, 1979; Biewener, 1982; Rubin & Lanyon, 1984). Rather, it appears that size-dependent changes in limb posture (larger animals have straighter limbs) may be a more general solution for stress similarity over a range of different-sized mammalian species (Biewener, 1983b).

Bone strain in the goat

Peak principal strains measured at the midshaft cranial and caudal cortices of the radius and tibia were similar in magnitude at the goat's fastest trotting speed (3.3 ms^{-1}) and maximum galloping speed (4.3 ms^{-1}). The difference in cranial tensile strains was less than 3 %, while the difference in caudal compressive strains was less than 9 %. Peak strain increased fairly linearly over the range of trotting speeds, fell 13 ± 4 % at the trot-gallop transition, and increased again only slightly at higher galloping speeds.

The distribution of strains recorded at the midshaft sites of the goat radius and tibia (cranial tension *versus* caudal compression) indicates that bending is the predominant source of strain (by a ratio of nearly 10:1). Indeed, only the equine metacarpus (Biewener, Thomason, Goodship & Lanyon, 1983a) has been shown to maintain overall axial compression during steady-speed locomotion. The predictability of this loading pattern (and orientation of peak principal strains, Table 2) for these two bones over the full range of gait and speed is similar to the dog and horse, and may enable reductions in bone mass required to resist the range of loads that must be supported (Biewener *et al.* 1983a; Rubin & Lanyon, 1982).

Bone strain and gait changes in the goat versus dog and horse

To test the hypothesis that bone mass and shape are selected to maintain a similar safety factor to failure (i.e. similar peak strains) at equivalent points in gait, we have compared the strain data obtained for the goats with that published for the radius and tibia of a dog of similar size (Rubin & Lanyon, 1982), and of horses 10-fold greater in body mass (Biewener *et al.* 1983b; Rubin & Lanyon, 1982).

Maximum trot versus maximum gallop within a species

The change in peak principal strain with increasing speed and change of gait is remarkably similar for these species. As with the goats, peak caudal midshaft strains developed at the fastest trotting speed recorded for the dog (radius: $-2384\ \mu\epsilon$, tibia: $-2006\ \mu\epsilon$) are similar in magnitude to those developed at the dog's top galloping speed (radius: $-2248\ \mu\epsilon$, $P < 0.05$; tibia: $-2016\ \mu\epsilon$, $P > 0.05$; Table 4). Although significant, the difference for the radius is only 6% (and, in fact, greater at a fast trot). While peak caudal midshaft strain in the radius is also similar in the horse compared at its fastest trotting and galloping speeds, peak caudal midshaft strain in the tibia is considerably greater ($P < 0.05$) at a maximal gallop than at the animal's top trotting speed. The maximum galloping speeds we obtained for these species on a treadmill under experimental conditions are somewhat low compared to the animals under natural conditions. This raises the possibility that peak strains, in fact, may be higher at a maximum gallop compared to a maximum trot.

We have based our comparisons among species on the peak compressive strains acting in each bone (caudal cortex in each case). Similar patterns are also found if the peak tensile strains acting in each bone (cranial cortex in each case) are compared. Peak principal tensile strains were typically 80–85% of the magnitude of peak compressive strains, due to axial compression counteracting the predominant bending that these long bones were subjected to. Because the tensile yield strength of bone is less than its compressive yield strength (120 MPa *versus* 160 MPa; see Currey, 1970, for a review), the safety factor of these bones, yielding in either tension or compression, is roughly three. Lanyon, Magee & Baggott (1979) have previously noted a similar finding in their study of the sheep radius, in which tensile strains were 70% of compressive strains, resulting from the distribution of axial and bending loads imposed on the bone.

Table 5. *Percentage differences and statistical comparisons of peak caudal midshaft strains at a maximum trot and at a maximum gallop between species*

Gait	Groups compared	Radius	Tibia
Fast trot	goat: dog	27 %, $P < 0.05$	11 %, $P < 0.05$
	goat: horse	15 %, $P < 0.05$	3 %, $P > 0.05$
	dog: horse	14 %, $P < 0.05$	13 %, $P < 0.05$
Fast gallop	goat: dog	18 %, $P < 0.05$	2 %, $P > 0.05$
	goat: horse	8 %, $P > 0.05$	37 %, $P < 0.05$
	dog: horse	11 %, $P < 0.05$	36 %, $P < 0.05$

When groups were different in size and had unequal variance (dog *vs* goat or dog *vs* horse), a modified Student's *t*-test was conducted to establish significance levels (Sokal & Rohlf, 1969).

Sample sizes are given in Table 4.

As we found in the goat, Rubin & Lanyon (1982) show a significant decrease in peak strain at the trot–gallop transition for the non-lead limb of the dog (Table 4). In the horse, a significant decrease in peak caudal midshaft strain was also recorded for the radius, but not in the metacarpus of the non-lead limb (Biewener *et al.* 1983a). Such a drop in peak strain (or stress) within limb skeletal elements suggests a redistribution or realignment of forces exerted on the limbs when an animal changes gait from a trot to a gallop. Exactly how such a redistribution of force might be achieved remains unclear, as conflicting data have been reported. In the present study, the distribution of strain due to bending *versus* compressive forces does not change markedly at the trot–gallop transition, indicating no major realignment of load borne by the bone. Pennycuik (1975) has argued that the average number of feet on the ground increases at the transition from a trot to a gallop, which would explain the drop in ground reaction force that has been recorded in various species (Biewener *et al.* 1983b; Cavagna, Heglund & Taylor, 1977). However, whereas a drop in duty factor of a limb (defined as the percentage of the stride period that a limb is in contact with the ground) occurs from a walk to a trot (Jayes & Alexander, 1978), correlating with the sharp increase in bone strain that has been observed, no such abrupt change in duty factor has been found at the trot–gallop transition (Biewener, 1983b; Jayes & Alexander, 1978; Rubin & Lanyon, 1982).

Comparison of bone strains between species at equivalent points of gait

In general, lower peak strains act in the goat limb bones at comparable points in the three species' gaits. While most interspecific comparisons of peak caudal-midshaft strain at a maximum trot and at a maximum gallop are shown to be significantly different, these differences are typically less than 20 % (Table 5). At a maximum gallop, peak strains are statistically similar only in the radii of the goat and horse, and in the tibiae of the goat and dog. At maximum trotting speed, peak strains are statistically similar only in the tibiae of the goat and horse. These interspecific differences in peak strains at equivalent points in gait are not that large given the potential for error due to: (a) variation in strain magnitude *versus* gauge site (shown to be 5–11 % for a distance of 15 mm in the present study), (b) individual variability

in strain (7% for goats and horses; peak strains for only one dog were reported for each bone) and (c) unknown differences in the performance levels achieved by the animals following surgical attachment of the strain gauges to the bones (no force plate data were reported for the dogs). Given these considerations, the data appear to show that despite differences in the number of bones, their geometries, the actual speed of gait, or the species, skeletal strains (or stresses) at equivalent speeds are similar.

In conclusion, the data presented here support, but do not confirm, our hypothesis that the range of speed within a trot and top speed of an animal are linked to the peak strains (or stresses) developed in its limb bones, such that animals of differing body size and with different speed ranges achieve similar skeletal safety factors at equivalent points of gait. The energetic cost of locomotion within a gait has been shown to be an important determinant of gait selection, minimizing cost at an intermediate 'preferred' speed within a gait for horses (Hoyt & Taylor, 1981). The comparison of peak bone strain made here indicates that mechanical factors also play a role in determining gait selection, performance capability and skeletal design. Peak skeletal strains of similar magnitude act in the goat and dog, because the dog has proportionately more bone resisting locomotor loads than the goat. Finally, it would be of interest to know whether peak stresses in muscle and tendon also show similar patterns with increases in speed and change of gait to those found here for bone stress. We are currently addressing these questions.

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