Analysis of a Tension/Compression Skeletal System: Possible Strain-Specific Differences in the Hierarchical Organization of Bone

JOHN G. SKEDROS, ROY D. BLOEBAUM, MARK W. MASON, AND
DENNIS M. BRAMBLE
*Bone and Joint Research Laboratories, V.A. Medical Center (R.D.B.), Division of
Orthopedic Surgery, University of Utah School of Medicine (J.G.S., M.W.M.), and
Department of Biology, University of Utah (D.M.B.), Salt Lake City, Utah*

ABSTRACT   *Background:* Examination of a simple skeletal cantilevered beam-like bone (artiodactyl calcaneus) suggests that regional differences in strain magnitude and mode (tension vs. compression) reflect regional adaptation in the structural/material organization of bone. The artiodactyl (e.g., sheep and deer) calcaneus has a predominant loading condition typified by the unambiguous presence of prevailing compressive and tensile strains on opposite cortices. Bone habitually loaded in bending may accommodate regional disparities in loading conditions through modifications of various aspects of its organization. These include overall bone build (gross size and shape), cross-sectional shape, cortical thickness, and mineral content.

Methods & Results: Cross-sections taken along the calcaneal body exhibited cranial-caudal elongation with the compression (cranial) cortex thicker than the tension cortex ($P < 0.01$). Mineral content (ash fraction) was significantly greater in the compression cortex ($P < 0.01$), averaging 6.6% greater than in the tension cortex. Strong positive correlations were found between mineral content and section location in both the tension ($r^2 = 0.955$) and compression ($r^2 = 0.812$) cortices. These correlations may reflect functional adaptations to the linear increases in stress that are known to occur in the distal-to-proximal direction in simple, unidirectionally loaded cantilevered beams. According to engineering principles, the roughly triangular transverse cross-sectional geometries and thicker compression cortex are features consistent with a short cantilevered structure designed to resist unidirectional bending.

Conclusions: Known differences in mechanical properties of bone in tension vs. compression suggest that these regional differences in cortical thickness and mineralization may be related to differences in strain mode. These structural/material dissimilarities, however, may be related to regional variations in strain magnitude, since bending and axially directed stresses in a simple cantilevered structure produce greater strain magnitudes in the compression domain. It is possible that the superimposed habitual strain magnitudes enhance strain-mode-specific adaptive responses. We hypothesize that these structural/material differences reflect the capacity of bone to process local information and produce a regionally heterogeneous organization that is appropriate for prevailing loading conditions.   © 1994 Wiley-Liss, Inc.*

Key words: Bone remodeling, Cortical bone, Bone mineral content, Skeletal adaptation, Rocky Mountain mule deer (*Odocoileus hemionus hemionus*)

Investigators suggest that one or a few strain features may be important in mediating bone growth and adaptation as well as homeostatic processes that maintain normal architecture and mechanical competence in the adult skeleton. Strain mode (e.g., tension vs. compression) is thought to be an important factor for

the following reasons: Cortical bone (1) is two to three times stronger in compression than in tension (Alexander and Bennet-Clark, 1977; Burstein et al., 1972, 1973; Reilly and Burstein, 1974, 1975); (2) yields at a higher strain in compression than in tension (Currey, 1970; Reilly and Burstein, 1974, 1975); (3) fails at the microstructural level by different mechanisms when loaded in tension and compression (Caler and Carter, 1989; Carter, 1982; Carter et al., 1981; Carter and Hayes, 1977; Currey and Brear, 1974); (4) is more fatigue-resistant in compression than tension (Carter et al., 1981; Pattin, 1991); and (5) accumulates fatigue-related microdamage at different rates in tension and compression (Caler and Carter, 1989; Carter et al., 1981; Carter and Hayes, 1977). Other aspects of strain such as strain magnitude (Carter, 1982; Goodship et al., 1979; Rubin and Lanyon, 1985), strain energy density (Brown et al., 1990; Carter and Hayes, 1976; Gross et al., 1991; Huiskes et al., 1987), and strain rate and distribution (Lanyon, 1987; Lanyon et al., 1982; O'Connor et al., 1982; Schaffler et al., 1989) have each been singled out as being important in maintaining a bone's architectural integrity.

In vivo strain magnitudes, strain modes, and other aspects of strain histories differ between regions of the same bone, but are all interrelated (Biewener, 1991; Biewener et al., 1986; Biewener and Taylor, 1986; Gross et al., 1991, 1992; Lanyon, 1974; Lanyon, 1984; Lanyon and Bourn, 1979; Lanyon et al., 1979; Rubin and Lanyon, 1982; Turner et al., 1975). Therefore, there is no clear consensus on whether one or several of these strain features is actually preeminent in maintaining skeletal mass and structural/material organization. Nonetheless, investigators postulate the existence of regional differences in bone tissue structural and material properties associated with regional differences in strain milieus (Beaupré et al., 1990; Biewener et al., 1986; Biewener and Taylor, 1986; Boyde and Riggs, 1990; Carter, 1982, 1984; Gross et al., 1991; Lanyon, 1981; Rubin, 1988; Rubin and Lanyon, 1985).

A simple loading condition that is thought to be associated with regional mechanically adaptive structural or material modifications is that characterized by a predominance of unidirectional bending stresses and the associated tension and compression strains predominating in different cortical regions (Bacon and Griffiths, 1985; Boyde and Riggs, 1990; Carando et al., 1989, 1991; Carter et al., 1981; Cowin, 1984; Currey, 1984a; Lanyon, 1980, 1981; Lanyon and Baggott, 1976; Portigliatti-Barbos et al., 1983; Skedros and Bloebaum, 1991). The objective of this study is to determine whether regions of cortical bone that sustain different habitual strain modes and magnitudes manifest corresponding adjustments in structural/material organization. We hypothesize that bone tissue subject primarily to compressive strain may exhibit significantly greater mineral content and/or increased cortical thickness when compared to bone tissue subject primarily to tensile strain.

MATERIALS AND METHODS

The artiodactyl (e.g., sheep, deer, and goats) calcaneus was selected for study since Lanyon (1973, 1974) showed it to be a simply loaded, natural (in vivo) tension/compression system (Fig. 1). By instrumenting
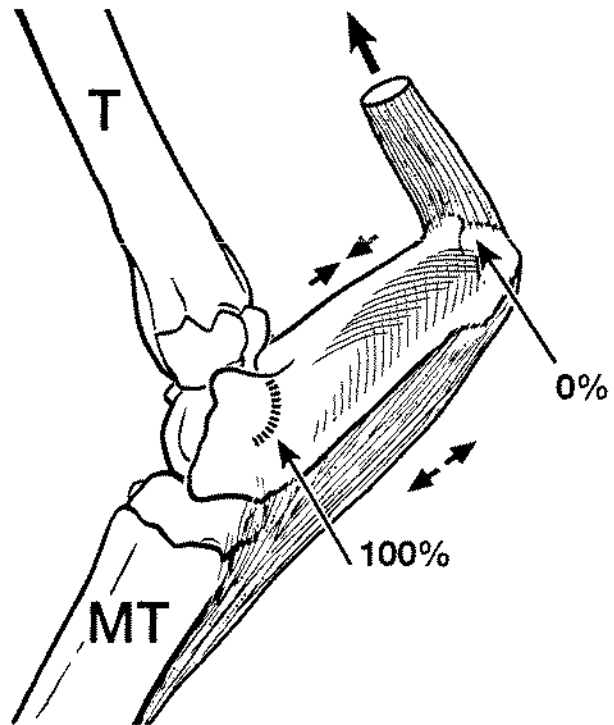

Fig. 1. Lateral view of right mule deer ankle region showing section locations, and major tendons and ligaments in situ. T = tibia; MT = metatarsus; % refers to percentage of bone "length"; 100% = proximal or "fixed" end. The stylized trabecular orientations are thought to approximate principal tension and compression stress trajectories (Lanyon 1974; Currey, 1984).

sheep calcanei in vivo with strain gauges, he showed that the cranial (dorsal) aspect receives prevailing compressive strain and the caudal (plantar) aspect receives prevailing tensile strains during typical loading. Lanyon's studies also showed that the magnitude of in vivo compressive strains measured on sheep calcanei were typically greater than the magnitude of tensile strains. The deer ankle (Fig. 1), like that of the sheep, goat, and other artiodactyls, is a uniaxial joint that confines flexion and extension movements to the sagittal plane (Alexander and Bennett, 1987; Schaeffer, 1947). Manipulations of partially dissected fresh deer and sheep ankle specimens with ligaments and tendons in situ, and examination of roentgenograms of the ankle of these animals in various degrees of flexion, revealed a range of motion that is virtually indistinguishable from those illustrated in roentgenograms of a living goat (Schaeffer, 1947) and described in living sheep (Getty, 1975; Lanyon, 1974). Therefore the deer calcaneus, which was available to us in large numbers, served as an appropriate model for this study.

Fifteen pairs of skeletally mature calcanei were procured from large wild male Rocky Mountain mule deer (Odocoileus hemionus hemionus) that had been taken to a game processing facility (Davis County, UT). Maturity was confirmed by the coossification of the distal calcaneal growth plate (Purdue, 1983). Examination of growth plates, as a means of determining skeletal maturity, does not eliminate the effects of age on mineral

content (Currey, 1984b; Trotter and Hixon, 1974) but does help to considerably narrow the degree of variation. At the time of specimen collection, the periosteal ("velvet") covering of the antlers had been shed and antler growth was complete. All specimens were from freshly killed (12 to 72 hours) animals that had been kept cool. The calcanei were manually cleaned of soft tissue and frozen at -20°C. Several weeks prior to further processing, one calcaneus from each pair was thawed and stored in 70% ethyl alcohol at room temperature (20°C).

To facilitate comparisons between calcanei of varying size, a calcaneal body (shaft) "length" was defined. Marks were made along the calcaneal body at 20, 30, 40, 50, 60, 70, and 80% of the defined length; the 80% mark being closest to the joint surface (proximal or "fixed" end of the cantilever). As illustrated in Figure 1, length was defined as the distance from inflection of the mid-articular surface (100% of length) to the point where the dorsal tubercle merges with the distal portion of the shaft (0% of length). A longitudinal axis was defined by two points that were marked at one-half the cranial-caudal distance at the 30 and 80% sections. The proximal end of each bone was securely fastened in a vice and cut transversely at each mark using a water-lubricated rotary saw with a fine-tooth, 0.89 mm diameter blade. A coring drill bit and a water-cooled drill press were used to obtain 2.5 mm diameter, cylindrically shaped cores of cortical (compact) bone from the compression (cranial) and tension (caudal) aspects of each section. Cores were removed at least 1 mm away from the subperiosteal surface. The immediate subperiosteal bone regions were avoided so that fibrous tissue associated with the plantar ligament insertion, which would artifactually lower mineral content, would not be sampled. Cores of compact bone were also obtained from the medial and lateral cortices of the 30 and 60% sections. Since the cortical bone at the 20 and 30% sections was typically thin (<2.5 mm), the cores from these sections consisted mostly of low porosity cancellous bone tissue. An additional core was removed from the floor of the pulley-like groove of the sustentaculum tali, containing the deep tendon of the m. flexor digitorum profundus. Manipulation of our morphologic prosections of deer hind limbs suggests that the sustentacular groove receives a prevailing restraining load from the tendon through a full arc of flexion and extension. Therefore, we surmise that this region is subject to prevailing compressive stress. Thus, bone from this region was used as an "internal control" for mineral content in compression. The ends of the cores from the sustentaculum tali were trimmed to remove cartilage and subchondral bone from the articular end, and to remove the thin veneer of cortical bone and soft tissue from the end forming the floor of the pulley-like groove. All cores from all of the sampled regions were between 4 and 6 mm in axial length. The method used for ashing bone was derived from methods described by Currey and Hughes (1973). Briefly, the cored specimens were thoroughly defatted in full strength chloroform, dried to constant weight (< 0.05% change), and ashed at 600°C for 24 hours. Ash fraction (mineral content) was calculated by dividing the weight of the ashed bone by the weight of the dried, defatted bone.

Subperiosteal to endosteal cortical thickness at cranial, caudal, medial, and lateral locations was measured to the nearest 0.01 mm by placing the tips of the jaws of a vernier caliper at the distal face of the cut surface of each section. Medial and lateral cortical thicknesses were measured at the midpoint of the cranial-caudal height of the medullary canal (see Fig. 2). Overall cranial-caudal heights and medial-lateral widths were measured at each section, the medial-lateral width being measured at one half of the cranial-caudal height of the medullary canal. All possible comparisons between each of the measured parameters were made between tension and compression cortices, between locations along one cortex, and between medial and lateral cortices. An alpha level of < 0.01 was considered statistically significant. Statistical significance was determined for each paired comparison using an analysis of variance (ANOVA) design. Least squares linear regression analyses of cortical thickness as a function of mineral content, and of each of these parameters plotted as a function of section location, were used to assess how these parameters changed along the calcaneal body. An analysis of covariance (ANCOVA) design was used to assess differences in slopes and intercepts of selected linear regressions (Sokal and Rohlf, 1981).

RESULTS

Cortical/Cancellous Distributions, Cross-Sectional Shape, and Bone Length

The cross-sectional shapes of sections taken along the calcaneal body resemble quasi-elliptical forms with the major axis oriented in the cranial-caudal direction (Fig. 2). Examination showed that the cortex of all but the compression aspect of the 80% section had some adherent cancellous bone tissue. The sections nearest the free (distal) end (i.e., 20 and 30% sections) were primarily of cancellous bone contained within a thin shell of cortical bone. The volume fraction of cancellous bone decreases as the articular surface is approached (Fig. 2). Ratios of mean cranial-caudal height to medial-lateral width progressively increased from the free end (30% section) toward the joint (fixed) end (70% section) (Fig. 3). The average calcaneal body length of the sample was 6.51 ± 0.26 cm.

Cortical Thickness

The 30 to 80% sections all displayed a significantly thicker compression cortex than the corresponding tension cortex ($P < 0.001$). The 20% section was the only exception, where the thickness of the compression and tension cortices was not significantly different ($P > 0.05$). The compression cortex progressively increases in thickness from the 30 to 80% section (Fig. 4). The thickness of the tension cortex exhibits a much smaller degree of increase from the free end to the joint (Fig. 4). Linear regression analyses of cortical thickness as a function of section location are highly correlated in both tension ($r^2 = 0.890$, $P < 0.002$) and compression ($r^2 = 0.969$, $P < 0.001$) cortices. There were no significant differences between medial and lateral cortical thickness from the 20 to 70% sections ($P > 0.05$). Only at the 80% section is the medial cortex significantly thicker than the lateral cortex ($P < 0.001$). The small differences between medial and lateral cortical thick-
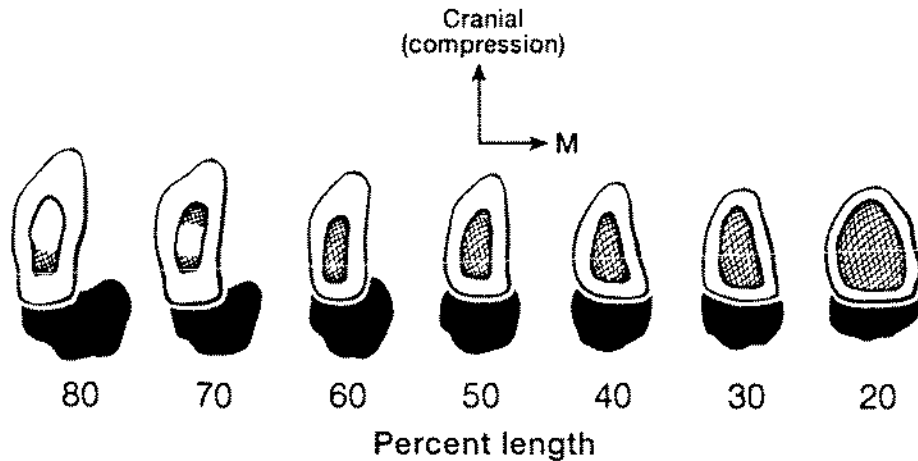
Cranial
(compression)

Percent length

Fig. 2. Representative cross-sections of a skeletally mature left mule deer calcaneus. The subperiosteal contour of the compression cortex is relatively narrowed along most of the calcaneal body, whereas the contour of the caudal (tension) cortex is rounded to nearly flat. The tension cortex is associated with a substantial mass of firmly adherent ligamentous and tendinous tissue, including the plantar ligament and tendon of the m. flexor digitorum superficialis.
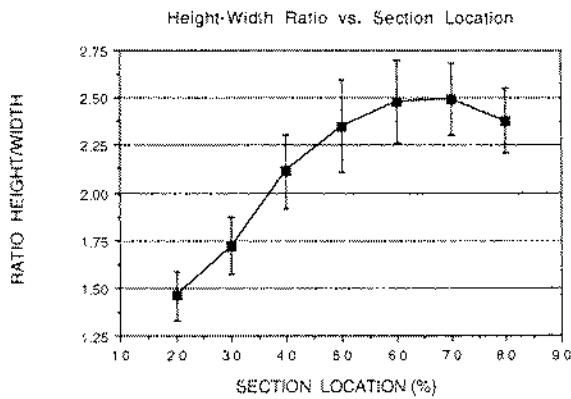

Fig. 3. Ratios of cranial-caudal height to medial-lateral width plotted as a function of section location show that the mule deer calcaneus progressively increases in cranial-caudal height from near the free end (20% section) to the 70% location.
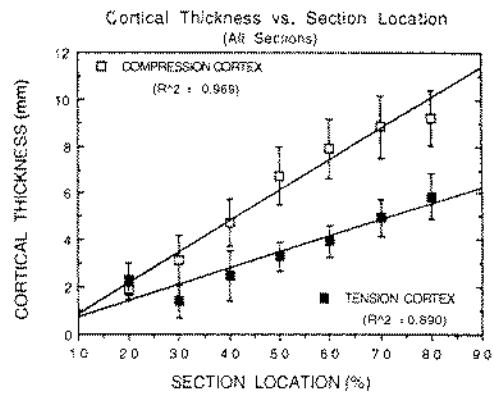

Fig. 4. Least square linear regressions of mean compression and mean tension cortical thickness vs. section location. ANCOVA shows that the slopes of these regressions are significantly different ($P <$ 0.0005).

ness in this region near the joint end of the calcaneal body can be partially attributed to geometric changes required for accommodation of the articular surface. The 80% section is therefore near the region where the cantilevered beam portion of the calcaneus begins to merge with the proximal articular end (Figs. 1,3).

Mineral Content

The mineral content of the compression cortex is significantly greater than the mineral content of the tension cortical bone at nearly all section locations (at 20, 30, 40, and 50% sections $P < 0.001$; at 60 and 70% sections $P < 0.01$; at 80% section $P < 0.05$) (Table 1). Along the compression cortex there are, with few exceptions, no significant mineral content differences between all possible pairings ($p > 0.05$). However, the 20% section, which is mostly trabecular bone, had significantly lower mineral content than each of the following sections: 50, 60, and 70% ($P < 0.01$). Similarly,

along the tension cortex there are, with few exceptions, no significant mineral content differences between all possible pairings ($p > 0.05$). Again, the 20% section shows significantly lower mineral content than the 50, 60, 70, and 80% sections ($P < 0.01$).

No significant differences are found between the mineral contents of the medial, lateral, and tension cortices of the 30% sections and the 60% sections ($P > 0.05$). However, as described above, there are significant mineral content differences between the compression and tension cortices at the 30 ($P < 0.001$) and 60% ($P < 0.01$) sections. In summary, these results show that at each section the compression cortex attains a significantly greater level of mineralization, averaging 6.6% greater, than the level of mineralization in the tension cortex (Table 1). Additionally, the medial, lateral, and tension cortices at the 30 and 60% sections exhibit a similar level of mineralization which is substantially less than the corresponding compression

TABLE 1. Ash fraction (mineral contents) at each section location; means and (standard deviations)[1]

Section	Tension	Compression	% Difference	Medial	Lateral	% Difference
20	62.40 (3.77)	67.04 (6.45)	+7.4			
30	64.51 (4.29)	69.50 (2.57)	+7.7	67.46 (4.21)	66.21 (2.83)	-1.9
40	65.32 (4.29)	70.11 (2.54)	+7.3			
50	66.54 (4.56)	72.28 (2.04)	+8.6			
60	67.15 (3.86)	71.36 (2.93)	+10.6	69.56 (3.68)	68.93 (5.57)	-0.9
70	66.89 (4.14)	70.96 (2.60)	+6.1			
80	66.75 (4.55)	69.87 (1.76)	+4.7			
ST	67.36 (2.78)	67.36 (2.78)				

[1]Percentages were calculated as a percent increase or decrease with reference to the tension or medial cortices, respectively. Compression−Tension/Tension × 100 or Medial−Lateral/Lateral × 100; ST = sustentaculum tali specimen.

cortex at these sections. Linear regression analyses of mineral content as a function of section location show correlated distal-to-proximal increases in both the tension ($r^2 = 0.776$, $P < 0.01$) and compression ($r^2 = 0.340$, $P = 0.17$) cortices (Fig. 5A). The correlations improve substantially if the analysis is restricted to the more "beam-like" 20 to 60% sections (compression cortex: $r^2 = 0.812$, $P < 0.04$; tension cortex $r^2 = 0.955$, $P < 0.004$) which excludes the regions potentially subject to more complex loading conditions (Fig. 5B). ANCOVA showed that the slopes of these beam-like regions are not significantly different ($P > 0.95$). Highest correlation coefficients were seen when all data points were fit to third order polynomial equations (Fig. 6). The maximum tension/compression mineral content differences occur at the 60% location and a convergence of the extrapolated curves is seen as the joint surface is approached. These findings support the possibility that the functional base of the "pure" cantilevered beam is near the 60% location. Linear regression analyses between tension and compression mineral contents at each section location also show a strong positive correlation ($r^2 = 0.780$, $P < 0.01$) (Fig. 7A). The correlation again improves substantially when the 70 and 80% sections are excluded ($r^2 = 0.922$, $P < 0.01$) (Fig. 7B). As discussed below, this implies a functional coupling between the two cortices.

The mineral content of the sustentaculum tali, a region which we surmise is primarily loaded in compression, is typically midway between the levels of mineral content in most of the compression and tension cortical locations (Fig. 6, Table 1). The cores taken from beneath the floor of the pulley-like groove of the sustentaculum tali consisted of low-porosity cancellous bone, which is typical of the bone near the subchondral regions of expanded joint surfaces (Currey, 1984b).

DISCUSSION

Although the artiodactyl calcaneus can be viewed as a cantilevered beam (Lanyon, 1973, 1974), its mechanical behavior is undoubtedly more complex. A simple cantilever beam subjected to a concentrated load at its distal end will sustain maximum bending stress and strain at the base where it joins its support. In the artiodactyl calcaneus, however, both anatomical relation and material properties suggest that only the outer 60% or so operates as a simple cantilever experiencing prevailing unidirectional bending loads. The most proximal region is unquestionably subjected to a more complex, directionally variable loading environment due to its close association with ligaments, tendons, the sustentaculum tali, and a specialized sliding articulation with the astragalas. We suggest that the linear changes in sectional geometry and mineral content from the 60% section (Figs. 3,5B,7B) to the free end of the calcaneus are related to the regional differences in strain mode and magnitude that would be expected to be present in a simple cantilevered beam.

The difference in cortical thickness and mineral content of the tension and compression cortices of the mule deer calcaneus, although suggestive of regional adaptation, is at variance with findings in other tension/compression bones. Lanyon and his co-workers showed in sheep tibiae that there are no differences in either peak principal strains or cortical thickness between the tension (cranial) and compression (caudal) cortices despite differences in prevailing strain mode (Lanyon and Bourn, 1979). In sheep radii, Lanyon and Baggott (1976) report that strains on the compressed (caudal) cortex are nearly twice the magnitude of those on tensile (cranial) cortex even though there is no difference in the thicknesses of these two cortices. Based on these findings they conclude that bone remodels to achieve a level of uniform stress, rather than strain, throughout the cortex (Lanyon, 1992; Lanyon et al., 1979). In sheep radii, they subsequently showed that the elastic modulus of the compressed cortex, in which strains are greater, is less than that of the tensile cortex and attribute this to a greater rate of remodeling, hence *lower* mineral content. The mineral content was 72.4 ± 0.27 ash fraction in the tension cortex and 70.8 ± 0.03 in the compression cortex in their sample of adult animals ($P < 0.01$). This finding is in contrast to the compressed cortex of the mule deer calcaneus which has both a *thicker* cortex and *higher* mineral content (hence lower rate of remodeling) than the tension cortex. Using horse radii, which have been shown in vivo to be tension/compression bones, Riggs et al. (1993a,b) demonstrated that the tension and compression cortices are not different in terms of mineral content. The differences between mineralization of tension and compression cortices of sheep radii and deer calcanei, and the lack of mineralization differences in sheep tibiae and horse radii, make interpretation of this data difficult. However, elastic modulus reflects the cumulative influences of several physical characteristics, including
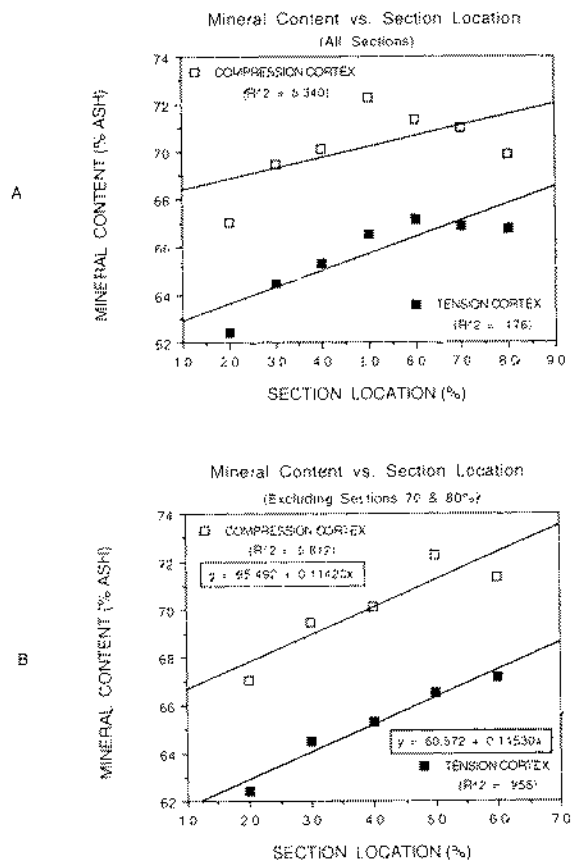
Fig. 5. Regressions of mean mineral content versus section location for both tension and compression cortices. A: all sections; B: excluding the 70% and 80% sections. Note the substantial improvement in the correlation coefficients when the more proximal sections are excluded. Regression equations are boxed. ANCOVA shows that the slopes are not significantly different ($P = 0.976$; where $P = 1.000$ shows no difference).

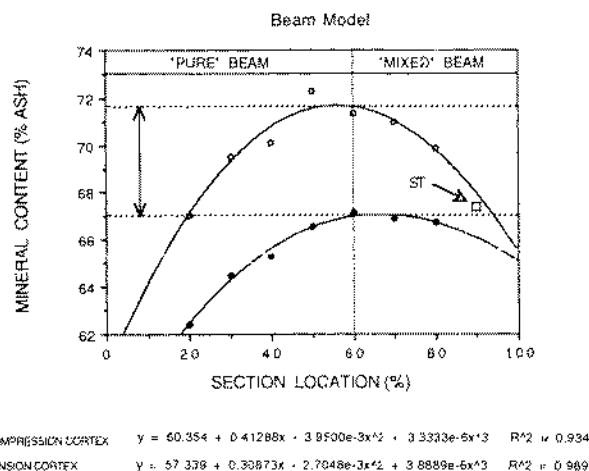|		
○ COMPRESSION CORTEX	$y = 60.354 + 0.41288x - 3.9500e\text{-}3x^2 + 3.3333e\text{-}6x^3$	$R^2 = 0.934$
● TENSION CORTEX	$y = 57.339 + 0.30873x - 2.7048e\text{-}3x^2 + 3.8889e\text{-}6x^3$	$R^2 = 0.989$

Fig. 6. Mineral content and section location data from all sections fit to third order polynomial equations. The double-headed arrow indicates the distance between the horizontal tangents of each curve. This is the predicted difference in peak mineral content. These curvilinear fits show the highest correlations in both tension ($r^2 = 0.989$, $P < 0.01$) and compression ($r^2 = 0.934$, $P < 0.01$) cortices. ST = mineral content of sustentaculum tali samples.

mineral content, porosity, collagen cross-linking, and collagen orientation. It is possible that different regions of bone can have similar elastic moduli even though these components are present in different proportions. In theory, bones from various anatomical locales may still achieve regional uniformity in some stress- or strain-related property by maintaining regional differences in cortical thickness, cross-sectional shape, mineral content, or in various other aspects of structural/material constitution.

It is important to note that the sheep tibia and sheep and horse radii do not have a tension member similar to the plantar ligament of the deer calcaneus. As discussed below, the presence of this structure may account for, or strongly influence, loading conditions, and thus the differences in mineral content, cortical thickness, and other aspects of the structural/material organization of the tension/compression cortices. If, however, the differences in mineral content in the tension/compression cortices of mule deer calcanei are actually strain-mode-specific, then the findings of Lanyon and co-workers in sheep tibiae and radii, and Riggs and co-workers in horse radii, may represent alternative structural/material adaptations for regional disparities

in strain mode and/or strain magnitude. It is unclear whether direct comparisons between short cantilevered bones and long limb bones are entirely appropriate at all levels of their hierarchical organization since bones from different regions of the same animal may also be sensitive to different levels (e.g., strain magnitudes or strain energy density) or qualities (e.g., strain mode or strain distribution) of stimuli (Beaupré et al., 1990; Bertram and Schwartz, 1991).

Functional Morphology and Biomechanical Roles of Bone Build, Shape, Cortical Thickness, and Mineral Content

Currey (1984a,b) suggests that the deformation at the free end of a short cantilevered bone depends much more on the strains near the fixed end than on those near the free end. It is also well known that simple plane straight cantilevers deformed by bending experience the greatest stress at the fixed end (Gere and Timoshenko, 1984). Therefore, from a biomechanical perspective, it is reasonable that natural skeletal cantilevers be designed to reduce stress near the fixed end (Currey, 1984a,b). This suggests that the tapered shape of the calcaneal body (Fig. 1), and the associated increase in cortical thickness and cranial-caudal height as the articular surface is approached may function as dual mechanisms for reducing deformation along the calcaneal shaft. The quasi-elliptical shape of the majority of the sections of the calcaneal body (Fig. 2) can be interpreted as an optimization of bone geometry for resisting both axial compression and bending stresses in the cranial-caudal plane. In a simple beam made of a homogeneous material and subject to axially directed loads, the magnitude of load which can be supported in compression is a function of the cross-sectional area and is unaffected by cross-sectional shape. In contrast, if this simple beam received an eccentric axial load resulting in bending deformation, then resistance to bending is strongly dependent upon cross-sectional
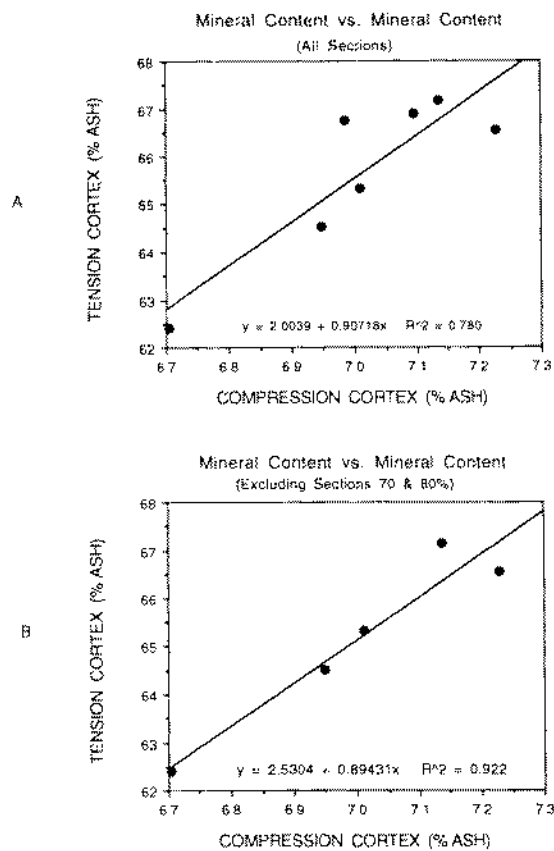
Fig. 7. Regressions of mean mineral content of the tension cortex vs. mean mineral content of the compression cortex at each section location. A: all sections; B: excluding the 70 and 80% sections. Note the substantial improvement in the correlation coefficients when the proximal two sections are eliminated. These proximal sections are from regions of presumably more complex loading conditions.

shape and the relatively thicker compression cortex may be an example of how cross-sectional shape and cortical mass function as dual mechanisms for limiting the degree of bending. However, the broad base of the tension cortex may also be related to the surface area needed for the attachment of the plantar ligament. A relative increase in medial-lateral width is especially notable at the distal end (e.g., 20 and 30% sections) where the gastro-soleus tendon forms a broad attachment. Increased complexities of loading conditions at both the proximal and distal ends of the calcaneal shaft may account for the deviation from the structural organization expected in a pure beam.

The possibility that the thicker cortex on the compression side may be adaptive is also supported by Burstein et al. (1972). They showed that when bone is subject to bending, it is possible to load to a higher stress on the compressive side than on the tension side. Thus, the thicker, more highly mineralized compression region of the deer calcaneus appears to have a greater capacity to accommodate this increased stress. In contrast, the medial and lateral cortices, which are not subject to a similar prevailing bending stress, show no differences in cortical thickness or mineral content. Evidence of mineral content adaptation between these cortices was not found, and would not be expected. However, mineral contents of the medial and lateral cortices, which lie in the low strains near the neutral axis, are not different from the mineral content at the tension cortices. How can this be reconciled? A plausible explanation, as suggested by Frost (1990) is that different strain thresholds for remodeling activity may exist in different cortical regions. Therefore, the medial and lateral cortices, although subject to lower strain magnitudes, may receive "regionally adequate" strains for the maintenance of their structural and material organization. It is possible that the higher mineral content in the compressive cortex is a reflection of adaptation enhanced by prevailing strain mode superimposed on markedly higher strain magnitudes.

The marked difference in mineral content between the tension and compression cortices may have substantial mechanical relevance. It is well established that small changes in bone mineral content can result in dramatic changes in mechanical properties, including "breaking" (fracture) stress (Vose and Kubala, 1959), bending strength (Currey, 1969), impact stress (Currey, 1969), fatigue life (Carter and Hayes, 1976; Schaffler and Burr, 1988), and elastic modulus (Schaffler and Burr, 1988). Extrapolating from these studies to the present work suggests that the greater level of mineral content of the compression cortex should make it two to three times stiffer and stronger than the tension cortex.

The strong positive correlations between mineral content, cortical thickness, and section location in the distal-to-proximal direction in both tension and compression cortices (Figs. 4,5) are suggestive of functional adaptation. We hypothesize that these changes in the "pure" beam portion of the calcaneus (Fig. 6) are related to the linear increases in prevailing stress which are known to occur in the distal-to-proximal direction in simple, unidirectionally loaded cantilevered beams (Gere and Timoshenko, 1984). Bone within the more proximal mixed beam region is presumably subjected

shape (Bertram and Biewener, 1988). The restricted degrees of freedom in the artiodactyl ankle complex limits these bending loads to a single plane. For beams so loaded, the optimal configuration is that which maximizes the second moment of area (I). Since $I = bh^3/12$, the material will be arranged to maximize the rigidity in the direction of the major axis of bending (h), hence an elliptical cross-section (Rubin, 1984; Wainwright et al., 1982).

The relatively thicker compression cortex may represent a mechanism for preferentially augmenting the cortical mass along the surface where it would be most effective in regulating bending deformation across the entire calcaneal body. Currey (1984a) suggests that it is advantageous for a simple cantilevered bone to have a lower habitual strain on the tensile side than on the compressive side. Furthermore, Currey (1984a,b) argues that in a beam-like bone, a quasi-elliptical or roughly triangular cross-section, with the apex of the triangle on the compression side, reduces strain on the tension side. Examination of representative cross-sections in Figure 2 shows that the essential features of this morphology are displayed by the mule deer calcaneus. Therefore, the quasi-elliptical cross-sectional

to much more complex and directionally variable bending loads. It is also noted that the mineral content of the compression and tension cortices at corresponding sections is well correlated along the beam-like portion of the calcaneal shaft (Fig. 7). These correlations imply a functional coupling between the opposing cortices. A plausible coupling mechanism may be related to the common relative strain magnitude that the material of the same section will have in a cantilevered beam subjected to a simple bending load. Alternatively, this coupling may reflect an arrangement aimed at keeping habitual tensile and compressive strains at the same proportion of their yield point (Currey, 1984a). The latter suggests that a uniform safety factor to failure may be the objective, or byproduct, of local differences in mineral content.

Biomechanical Roles of Associated Soft Tissue Structures

Various soft tissue structures associated with the artiodactyl calcaneus are probably also important in the biomechanical functioning of this system. These structures, the plantar ligament and the tendon of the m. flexor digitorum superficialis, are likely to carry substantial tensile loads and thereby reduce bone deformation. The thick fibrous tissue mass along the tension cortex can readily be appreciated by examining the sections in Figure 2. Although the main function of the plantar ligament is to limit excessive joint excursion, it probably also stores elastic strain energy during locomotion (Alexander, 1982; Alexander and Bennet-Clark, 1977; Alexander and Dimery, 1985; Currey, 1984b; Dimery et al., 1986; Ker, 1981; Morgan et al., 1978). Since the plantar ligament and the associated flexor tendon are intimately and firmly attached to the tension cortex, the latter is best considered a "fibro-osseous cortex." Because this fibro-osseus constitution may modify local and regional loading conditions, the foregoing biomechanical and elastomechanical interpretations must be considered provisional since only the osseus component of the tension cortex was emphasized. Additionally, inclusion of these tension members is likely to displace the neutral axis of bending toward the tension cortex and away from the compression cortex. A direct consequence of such a shift would be a magnification of the compressional stress on the opposite cortex, and attenuation of the tensional stress on the cortex adjacent to the tension members.

In the mule deer calcaneus, the tapered shaft, elliptical to roughly triangular cross-sectional shapes, thicker compression cortex, differences in mineralization between the compression and tension cortices, and associated soft tissue tension members, all interact to contribute to the functional organization of this bone. According to engineering principles, this organization is expected to reduce bending in a short cantilever. Mineral content and cortical thickness differences may reflect remodeling differences in a bone that, although designed to be a stiff cantilever, must simultaneously accommodate habitual regional differences in strain mode, magnitude, and possibly other strain-related features.

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