Mechanical Significance of Femoral Head Trabecular Bone Structure in *Loris* and *Galago* Evaluated Using Micromechanical Finite Element Models

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**ABSTRACT**

Work on the interspecific and intraspecific variation of trabecular bone in the proximal femur of primates demonstrates important architectural variation between animals with different locomotor behaviors. This variation is thought to be related to the processes of bone adaptation whereby bone structure is optimized to the mechanical environment. Micromechanical finite element models were created for the proximal femur of the leaping *Galago senegalensis* and the climbing and quadrupedal *Loris tardigradus* by converting bone voxels from high-resolution X-ray computed tomography scans of the femoral head to eight-noded brick elements. The resulting models had approximately 1.8 million elements each. Loading conditions representing takeoff phase of a leap and more generalized load orientations were applied to the models, and the models were solved using the iterative “row-by-row” matrix-vector multiplication algorithm. The principal strain and Von Mises stress results for the leaping model were similar for both species at each load orientation. Similar hip joint reaction forces in the range of 4.9 to 12 body weight were calculated for both species under each load condition, but the hip reaction values estimated for *Loris* were higher than predicted based on locomotor behavior. These results suggest that functional adaptation to hip joint loading may not fully explain the differences in femoral head trabecular bone structure in *Galago* and *Loris*. The finite element method represents a unique and useful tool for analyzing the functional adaptation of trabecular bone in a diversity of animals and for reconstructing locomotor behavior in extinct taxa.

Recent work on the interspecific variation of trabecular bone in the proximal femur of extant primates has revealed important architectural differences between taxa with divergent locomotor behaviors (Fajardo and Müller, 2001; MacLatchy and Müller, 2002; Ryan, 2001; Ryan and Ketcham, 2002b; but see Viola, 2002). It is generally thought that, just as with external bone anatomy and diaphyseal cross-sectional geometry (Anemone, 1990; Connour et al., 2000; Demes and Jungers, 1989), this variation reflects differences in joint loading and limb use during various activities. It is not known, however, whether these structural differences can be fully explained as the result of epigenetic or evolutionary functional adaptation, or whether other nonstructural causes such as genetic, nutritional, hormonal, or gender factors may play a role as well.

Experimental and modeling work over the past few years has further developed our understanding of the mechanisms of bone modeling (Huiskes et al., 2001; Huiskes et al., 2000). This response is facilitated by the process of mechanotransduction, involving the lacuno-canicular porosity of the bone matrix (Burger and Klein-Nulend, 1999). A reasonable hypothesis that follows from these observations, assuming general similarity across mechanosensory cells, is that stresses and strains at the trabecular bone tissue level should be distributed rather evenly over the trabecular architecture within a specific mechanically homogeneous

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region. Although there may be some variation across a structure depending on the specific loading environment of a bone or region (Hsieh et al., 2001), especially in bones such as the femur, as well as over the lifetime of an animal, this hypothesis implies that in a perfectly adapted structure, all bone is loaded at the same physiological strain level. While the prediction of uniform strain distribution seems reasonable, the magnitudes of these strains could vary quite widely across different regions, individuals, and species, depending on various genetic and epigenetic factors as well as differences in the operative function of bone.

Recently introduced imaging and numerical techniques have enabled a quantitative evaluation of physiological bone tissue strains in whole bones (van Rietbergen et al., 1999, 2003). In these studies, microfinite element (μFE) models were used to calculate the tissue-level stresses and strains in bone using a three-dimensional (3D) model generated from high-resolution cross-sectional images that can represent the trabecular architecture of the bone at the submillimeter level (van Rietbergen et al., 1995). Using these models, remarkable similarities in tissue-level stress/strain distributions were found for the canine and human femur, with strains varying only in a limited range for physiological external loading conditions (van Rietbergen et al., 1999, 2003). In neither of these studies was a perfectly uniform tissue stress/strain distribution found, but this seems reasonable, given the fact that the bone at this site is not adapted to a single load direction. These studies provided detailed quantitative information about the bone tissue strains that can be expected in load-adapted femoral bone structures, and provide a basis for continued analyses of bone tissue strain and functional adaptation in other animals.

Here we investigate the mechanical behavior of femoral head trabecular bone in the slender loris, *Loris tardigradus*, and the Senegal galago, *Galago senegalensis*, using μFE techniques. These animals were chosen because clear differences in the 3D femoral head trabecular bone structure were found and appear related to differences in locomotor behavior (Fig. 1) (Ryan and Ketcham, 2002b). As compared to lorises, who have relatively isotropic trabecular bone throughout the femoral head, galagos have a less dense and more anisotropic trabecular structure. Distinct differences in locomotor behaviors and external locomotor anatomies have been noted between the specialized, saltatory galagos and the slow quadrupedal and climbing lorises (Anemone, 1990, 1993; Connour et al., 2000; Demes and Junger, 1993; Gebo, 1987; Runestad, 1997). Although measurements of hip joint forces are not available, the magnitude and orientation of joint loading in these two taxa is expected to be quite different, especially considering the large differences in hindlimb ground reaction forces generated during locomotion (15 times body weight in *Galago senegalensis* vs. 0.5–1.0 times body weight in *Loris*; Demes et al., 1990, 1993; Gunther, 1985; Ishida et al., 1990) and the differences in locomotor kinematics (Burr et al., 1993; Gebo, 1987; Runestad, 1997; Zienkiewicz, 1977). This technique has been recently used to answer questions in

**THE FINITE ELEMENT METHOD**

The finite element method (FEM) is a mathematical modeling technique used widely in engineering structural analyses as well as biomechanical analyses (Baran, 1988; Beaupre et al., 1986; Huiskes and Chao, 1983; Huiskes, 1993; Kolston, 2000; Koriath and Versluis, 1997; Zienkiewicz, 1977). This technique has been recently used to answer questions in
physical anthropology (Chen, 1995; Chen and Povirk, 1996; Edelman and Reeke, 1996; Korioth et al., 1992; Korioth and Versluis, 1997; Richmond and Qin, 1996; Ross et al., 2002; Ryan, 1997; Ryan et al., 1996; Strait et al., 2001, 2002), and holds great promise as a means of testing hypotheses regarding the mechanical design of skeletal structures in extant and extinct primates. The FEM is a unique tool in functional morphological and paleoanthropological research because it is a powerful and nondestructive modeling method that, when used in conjunction with more traditional comparative morphological analyses, can produce useful insights into organismal design. Perhaps the greatest value of FEM is that it allows the researcher to experimentally manipulate models to test hypotheses that otherwise would be impossible to test on living subjects or fossil specimens.

FEM is a numerical method of estimating the unknowns of the governing differential equation at discrete points in a continuous physical system (Huiskes and Chao, 1983; Zienkiewicz, 1977). The technique is capable of solving complex problems by redefining those problems as a series of simpler, interrelated approximations (Korioth and Versluis, 1997). A finite element analysis involves modeling an infinitely complex system by replacing the governing differential equations with a discrete system of algebraic equations (Korioth and Versluis, 1997). Such a replacement results in a model with a finite number of degrees of freedom and one which can be relatively easily solved.

Using FEM in biomechanics is based on the very basic mechanical principle that when a structure is loaded, stresses are generated in its materials (Huiskes and Chao, 1983). The exact nature of these stresses (aspects such as their magnitude, distribution, and orientation) will be determined by the nature of the loads, the geometry of the object, and the properties of its materials. FEM utilizes this concept to model all of these aspects of a mechanical system, and to approximate the nature of the stresses in the structure. To this end, Beaupre and Carter (1992) defined three basic steps in using FEM in structural analyses: model creation, model solution, and validation and analysis of results.

The first step, model creation, involves describing all aspects of the object mathematically, including the geometry, material properties, forces, and boundary conditions. Any object can be modeled with FEM by dividing the object into a number of smaller blocks or elements which are connected at points called nodes. This process of creating an element mesh by subdividing the object into smaller elements is known as discretization (Beaupre and Carter, 1992). A variety of elements are available for modeling, including various two-dimensional (2D) and three-dimensional (3D) types. The specific element type (2D or 3D) and the particular shape (e.g., cubic or tetrahedral) to be used depends on the type of model to be created and solved.

With the object geometry described, all other physical aspects of the system are then defined mathematically. Material properties which describe the mechanical behavior of the constitutive materials must be assigned to each element. Among the most important of these properties are Young’s modulus and Poisson’s ratio. Young’s modulus (E), or the elastic modulus, is a measure of the stiffness of a material and is defined as $\sigma/\varepsilon$ (stress/strain) (Wainwright et al., 1982). Poisson’s ratio ($\nu$) is a measure of the ability of a material to resist change of volume and change of shape, and is determined by dividing the lateral strain by the axial strain (Wainwright et al., 1982).

The definition of the material properties will depend on the behavior of the material being modeled. Bone is often modeled with either transverse isotropy or orthotropy (Beaupre and Carter, 1992). For the former model, which may be an accurate representation for cortical bone, five constants are needed including two Young’s moduli (longitudinal and transverse), two Poisson’s ratios, and one shear modulus (Beaupre and Carter, 1992). By contrast, an orthotropic material with three orthogonal axes of symmetry requires nine constants: one Young’s modulus, one Poisson’s ratio, and shear modulus in each of the three orthogonal planes (Beaupre and Carter, 1992).

The final step in model creation is the definition of the boundary conditions and loads, both of which are applied at the nodes. Boundary conditions take the form of constraints on movement, preventing rigid body motion. These conditions are typically applied far from the areas of interest to prevent stress artifacts from the constraints. The applied loads are typically joint, muscle, and ligament forces that are generated during some realistic or hypothetical activity pattern. The exact loading conditions, both magnitude and orientation, will depend largely on the particular goal of the model and the questions to be answered.

Once the model has been created, the second step is model solution. To solve the model, the equations that govern force equilibrium at each node are solved. The system of equations is given by:

$$\{F\} = [k]\{u\}$$  \hspace{1cm} (1)$$

where $\{F\}$ is the vector of nodal forces, $[k]$ is the global stiffness matrix which is constructed from the stiffness matrices of each element, and $\{u\}$ is the vector of nodal displacements (Beaupre and Carter, 1992; Korioth and Versluis, 1997). It is the nodal displacements which are solved given a set of nodal forces, constraints, and the global stiffness matrix. It is important to note that these equations describe force equilibrium at the nodal points, and therefore are only approximations of the exact solution. The accuracy and validity of any FE model, therefore, are constrained both by the mesh density (the number of elements and nodes) and by the accuracy of
approximation of the material properties and loading conditions.

The element stiffness matrix defines the stiffness relations between the degrees of freedom, and is constructed from the material properties of the elements (van Rietbergen et al., 1996b). This matrix is positive definite, symmetric, and usually sparse (van Rietbergen et al., 1996b). The size of this matrix is related to the number of nodes and the number of degrees of freedom at each node. The total number of degrees of freedom for a model is determined by multiplying the number of degrees of freedom at each node (three for a 3D model) by the number of nodes. The size of the stiffness matrix is then the square product of the number of degrees of freedom, and can be quite large for large models (van Rietbergen et al., 1996b).

For very large models, the size of [k] may be prohibitively large, even with modern computational techniques. Therefore, new methods were developed that allow solution of very large FE models through an iterative element-by-element (EBE) approach (van Rietbergen et al., 1995, 1996b). These new methods utilize the preconditioned conjugate gradient method and several memory-reducing techniques to solve Equation (1). Each iteration in this technique requires the multiplication of [k] by a direction vector p. An EBE technique is employed to eliminate the need for computing the entire global stiffness matrix, allowing multiplication of [k]*p at the element level. In addition, if all elements are the same size and have the same orientation (usually no orientation since they are cubic), then the global structure is described by connectivity alone, and no coordinate data must be stored. The last memory-saving implementation is the assignment of uniform material properties to all elements. In such a case, only one element stiffness matrix must be constructed and stored rather than a different one for each material.

This FE technique is used for analyses of trabecular bone because it allows the use of high-resolution imagery (either X-ray CT or serial thin sections) to construct highly accurate FE models from voxel data. These models utilize a voxel conversion method to create one brick element for each voxel, and achieve a resolution on the order of 20–100 μm on a side for each element (Kabel et al., 1999b,c; Odgaard et al., 1997; Ulrich et al., 1998; van Rietbergen et al., 1995, 1996a,b, 1999). Using the EBE approach, these researchers were able to construct and solve 3D models ranging in size from several hundred thousand elements to close to 100 million elements.

The FEM is a computer modeling technique, and as such, its utility in analyses is limited by the variables used to construct the model. In modeling a physical system precisely, it is important to establish both the validity and the accuracy of FE models (Huiskes and Chao, 1983). The validity of a model refers to the precision with which the mathematical variables (loading conditions, boundary conditions, and material properties) describe the actual behavior of the structure. The validation of a model entails determining the degree to which the model with all of its mathematically described features approximates reality. Because the FEM is a modeling technique, it justifiably necessitates multiple simplifying assumptions. It is through comparison to empirically determined data that a model’s validity can be checked.

The accuracy of an FE model refers to the degree to which the FE mesh approximates the correct solution for the model. The fact that the initial process of discretization results in reducing an infinitely complex system to a finite and solvable system necessitates an assessment of model accuracy. A model’s accuracy can be checked by performing a convergence test (Beaupre and Carter, 1992; Huiskes and Chao, 1983). This test is based on the fact that any FE model converges to the exact solution as the number of elements and nodes increases toward infinity. By refining the FE mesh and checking the results, the accuracy of the initial model’s results can be established.

MATERIALS AND METHODS

High-resolution X-ray computed tomography scanning

The right femur of one Galago senegalensis and one Loris tardigradus individual was chosen from a larger taxonomic sample used in the analysis of interspecific variation of trabecular structure in living prosimian primates (Ryan, 2001; Ryan and Ketcham, 2002b). The Galago specimen was from the osteological collection of the National Museum of Natural History (Washington, DC), and the Loris was from the collection of the American Museum of Natural History (New York, NY). Both individuals were wild-shot adults. The two specimens used were representative of typical fabric structures for their respective species, with the Galago being relatively anisotropic (degree of anisotropy of 7.347 in the inferior half of the femoral head), and the Loris individual being relatively isotropic (degree of anisotropy of 1.386 inferiorly), as quantified using the star volume distribution method (Fig. 1) (Cruz-Orive et al., 1992; Karlsson and Cruz-Orive, 1993; Odgaard, 1997; Ryan and Ketcham, 2002b). The exact body masses for the specimens used were unknown, but the species mean values of 283 g for Galago and 267 g for Loris were taken from the literature (Smith and Junger, 1997).

Serial scan data were collected from each femur, using the high-resolution X-ray computed tomography (HRXCT) scanner at the University of Texas at Austin (UTCT; http://www.ctlab.geo.utexas.edu), with a slice thickness and slice spacing of 36 μm. Scans were collected beginning from the most proximal portion of the bone (either the head or the greater trochanter) and proceeding to just below the
head. This protocol produced 168 and 171 slices for the proximal femur for Galago and Loris, respectively. Specimens were scanned with source energy settings of 180 kV/0.133 mA, 130% offset, and 63-mm source-object distance. The field of view was 25.4 mm, yielding an inline pixel size of 24.8 μm. The UTCT scanner was calibrated for dimensional accuracy within 0.5% in both the center and edge of the field of reconstruction, indicating no significant image distortion (Ryan, 2001). Once the scan data were collected, images were reconstructed and saved in TIFF format. Each slice image in the scan datasets was resampled to equalize the inline and inter-slice values to obtain cubic voxels. Although resampling the datasets resulted in a loss of resolution in the x,y plane, the voxel resolution was still well within the range in which trabecular structures can be accurately reconstructed and quantified (Kothari et al., 1998). The range of trabecular thickness in the extant strepsirrhine sample used in earlier work was from 118–161 μm (Ryan and Ketcham, 2002a), which is much larger than the voxel resolution.

**μFE analyses**

For each image stack, two small platforms were constructed and merged with the bone datasets on the superior and anterior sides of the voxel grid positioned over the center of the femoral head. Each platform extended to the superior and anterior surfaces of the voxel grid and acted as the site of application of the loads for each model. In all models, loads were applied perpendicular to the face of the platform and were distributed evenly across the face of each platform.

The data stacks were segmented using values determined from an iterative thresholding technique (Ridler and Calvard, 1978; Trussell, 1979). The optimal threshold was calculated using the grayscale histograms of the images by iteratively determining the “mean” background and “mean” object gray values and then taking the mean of these two values. At each iteration, the previously determined threshold (the calculated average of the background and object gray values) was used as a comparator to define the object and background elements within the original image. A new threshold value was determined at each iteration based on this comparison, and iteration continued until a stable threshold value was found. Data collected with the HRXCT scanner used in this study were validated for trabecular bone studies with another segmentation algorithm and shown to be accurate relative to histological sections (Fajardo et al., 2002). Additionally, the thresholding routine used here was shown to produce accurate segmented images for use in studies of trabecular bone (Ryan, 2001).

The resulting data grids were 10.8 × 6.66 × 6.16 mm for Galago and 10.0 × 6.67 × 6.03 mm for Loris, which included the entire proximal femur and the “empty” space between the bone and the grid edges. A large-scale FE-model was constructed by converting each voxel in the three-dimensional reconstructions to an eight-noded brick element, each of which had an edge length of 36 μm. The resulting FE-model for the Galago had 1,750,047 elements and 2,189,367 nodes. The Loris model had 1,855,125 elements and 2,227,460 nodes. All elements were assigned linear elastic isotropic material properties with a Young’s modulus of 15 GPa and a Poisson’s ratio of 0.3, as used in earlier studies (van Rietbergen et al., 1999). The same material properties were used for trabecular bone, cortical bone, and the two loading platforms. Each model was processed using an iterative FE-solver, implementing the “row-by-row” matrix-vector multiplication algorithm (van Rietbergen et al., 1996a,b) running on the SGI Cray SV1 Parallel Vector Supercomputer located at the University of Texas at Austin. Processing took anywhere from 15–20 hr per model.

Different loadcases were successively applied to the models to represent different activities. The first loadcase was designed to assess tissue stress and strain distribution in the Galago and Loris femora by simulating the loads generated in the Galago during the takeoff phase of a leap. Despite previous measurement of ground reaction forces in the leaping Galago, not much is known of the orientation or magnitude of forces at the hip joint in these primates. Based on measured hip joint forces during various activities in a variety of other animals (Bassey et al., 1997; Bergmann et al., 1984, 1993, 1995; Page et al., 1993) and the kinematics of the leap in Galago (Aerts, 1998; Gunther, 1985), a load of five times body weight (BW) (13.85 N for Galago; 13.05 N for Loris), positioned at an angle of 37° anterior to the superoinferior axis in the parasagittal plane, was applied to each model (Fig. 2). No mediolateral force component was included in these loadcases.

Both models were loaded to simulate simplified loading conditions during the takeoff phase of a leap in the galago, because this loading regime is considered to be the one in which the highest joint loadings would be engendered in either animal during “normal” activity. Additionally, loading the models in the same way allows the trabecular architecture to be isolated as the “unknown” variable. The μFE models therefore function as experiments to test the
that the mean strain magnitudes are generally similar across different sites and individuals. In the two previous studies (van Rietbergen et al., 1999, 2003), mean strain values of 304 μstrain for the human and 279 μstrain for the canine femoral head trabeculae were obtained. The value for the human femur of 304 μstrain was used here to scale the original hip joint forces to calculate the force magnitude that produces a comparable physiological bone tissue strain distribution using the equation:

\[
F_{\text{joint}} = \frac{\varepsilon_{\text{phys}}}{|\varepsilon|_{\text{VOI}}} \cdot F_{\text{ini}} = \frac{304 \text{ μstrain}}{|\varepsilon|_{\text{VOI}}} - 5 \times BW \quad (2)
\]

with \(F_{\text{ini}}\) the initially applied load, which was 5 × BW for each loadcase. In effect, either value could have been chosen, but the higher human value provides a theoretical upper limit for the scaled joint force values and allows comparison with both human and canine models.

**RESULTS**

The contour plot of the \(|\varepsilon_{\text{principal}}|\) for the 37° 5 × BW load for each model shows how the loads are transmitted through the femoral head under this simplified loading scenario (Fig. 4). These contour plots indicate that the superoinferiorly oriented trabeculae are loaded in compression, while the mediolaterally oriented trabeculae appear to be primarily loaded in tension, corresponding well to the results of the previous canine and human femoral head models.

The hip joint magnitudes that would produce an average tissue strain magnitude of 304 μstrain, as calculated from Equation 2, for the 37° loadcase were found to be very similar for both taxa: 8.8 × BW for Loris, and 8.3 × BW for Galago. After scaling the results for these hip joint force magnitudes, the distributions of principal strain and the Von Mises equivalent stress in the two models were remarkably similar (Fig. 5). The galago had somewhat higher tensile strains, but the difference was minimal. The low percentage of tissue with zero strain for either the Galago or the Loris models indicates that essentially all trabeculae are load-bearing within the central portion of the femoral head, where the VOI was positioned. The summary statistics for the principal strain and Von Mises stress for each of the loadcases show the results for the two species (Table 1).

When the load orientations were varied, some differences between taxa emerged. Using Equation (2), a different scaling factor was found for each load direction (Table 1). Based on these calculations, predicted hip joint forces varied from about 4.9 × BW when the load was acting in the anterior direction, to about 12 × BW for the superior direction (Fig. 6a). After scaling the histograms for each load angle to the respective force magnitudes, the standard deviations of the absolute values of the principal strain distribution \(\varepsilon_{\text{VOI}}\) were calculated. Standard deviations were consistently somewhat lower in Galago.
than in Loris, suggesting that for all load directions, the strain distribution in Galago is more uniform than in Loris (Fig. 6b). For both taxa, the lower standard deviations, and thus the most uniform strain distribution, were found for the anterior loading direction, but these differences were small. The maximum Von Mises stress found in the bone tissue after scaling the hip joint force shows higher values for Loris when the load acts superiorly, and higher values for Galago when the load is acting at angles between 30–90° (Fig. 6c). For loads acting in the anterior direction, a very similar maximum Von Mises stress was found for both taxa. The scaled principal strain distributions for each of the four angled loads (0°, 30°, 60°, and 90°) are plotted in Figure 7. The distribution of εVOI changes at each load orientation, but the distributions are quite similar in both Galago and Loris.

**DISCUSSION**

The fabric anisotropy of trabecular bone in the proximal femur of lorisids and galagids was shown to be significantly different in two independent studies (MacLatchy and Müller, 2002; Ryan and Ketcham, 2002b). Just as with the variation in external femoral head shapes as well as diaphyseal cross-sectional morphology in these taxa (Anemone, 1990; Connour et al., 2000; Demes and Jungers, 1989), these architectural differences in trabecular bone appear to track locomotor behavioral differences closely. Considering the proposed mechanical significance of trabecular bone structure, the relation of this architectural variation to the hypothetical differences in the magnitude and orientation of the loads generated at the hip joint during locomotion makes intuitive sense. In spite of these apparent locomotor signals in trabecular structure, the functional morphology of the proximal femur in strepsirrhines, especially in relation to the structure and function of the femoral neck, remains uncertain. In contrast to the situation in anthropoids (Rafferty, 1998), Demes et al. (2000) found no relationship between locomotor behavior and femoral neck cortical bone structure in strepsirrhines, suggesting that cortical and trabecular bone morphology may present different functional signals in this region.

Given the somewhat complex relationship between trabecular bone morphology in the proximal femur and locomotor behavior, the actual mechanical significance of structural differences, as well as the physiological mechanisms driving the structural variation, remain unclear. The observed morphological variation in trabecular structure in strepsirrhines could result from a number of structural or nonstructural physiological factors, including strain-induced modeling or remodeling, differences...
in developmental biology of the proximal femur between these groups, hormonal or genetic constraints, or a combination of several of these (for a review see Lovejoy et al., 2002). The divergence of galagos and lorises at least 40 Myr ago (Seiffert et al., 2003) clearly provides ample time over which these taxa diverged not only anatomically, but also developmentally and physiologically.

Given these considerations and the anatomical and trabecular structural differences between galagids and lorisids, the primary goal of this study was to estimate tissue stress and strain in the femoral head trabecular bone in one Loris and one Galago specimen, and in so doing, gain an initial insight into the mechanical and adaptive significance of variation in trabecular architecture in these animals. Due to the small sample sizes, the lack of direct model validation, and the other simplifying assumptions used here, the functional conclusions based on these models must necessarily be limited.

With these limitations in mind, the results of these models suggest that despite significant differences in trabecular bone structure within the femoral heads of these two individuals, the tissue stress and strain values do not differ significantly across multiple load orientations. At all of the investigated orientations, a physiological strain distribution was obtained for the centrally placed trabecular bone VOI. The estimated hip joint force magnitude ranged from 4.9 × BW for a joint force oriented in the anterior direction to about 12 × BW for a force in the superior direction. In all cases, the standard deviation of the distribution was less than that reported in earlier studies for the human femur (185 μstrain) and the canine femur (212 μstrain) (van Rietbergen et al., 1999; van Rietbergen et al., 2003), indicating that a more uniform strain distribution was obtained in the femoral heads of these nonhuman primates.

For all estimated hip joint forces, very similar values were predicted for the bone tissue Von Mises stress, with a range of 4.95–5.19 MPa. These results differ less than 13% from the values found for the average Von Mises stress in the earlier canine (4.60 MPa) and human (4.66 MPa) studies (van Rietbergen et al., 1999, 2003). It is interesting to note that, had we taken the average strain of 279 μstrain from the canine as the reference, the predicted Von Mises stress would have been in the range of 4.54–4.76 MPa, and thus would have been in perfect agreement with the calculated canine and human femur values. In all cases, the maximum Von Mises stress in the bone of between 17.2–29.9 MPa was less than the reported bone tissue fatigue strength of 100–140 MPa (Choi and Goldstein, 1992), indicating a high safety factor of about five, assuming similar yield strength in these animals.

A second purpose of the current study was to investigate whether the calculated hip joint forces reflect differences in locomotor behavior between the taxa. The hip joint force range of 4.9 × to 9.6 × BW seems reasonable for the leaping Galago, whose locomotor behavior is strongly hindlimb dominant. By contrast, the range of 6.0 × to 12 × BW for Loris seems too high for a slow quadruped. Ground reaction forces on the hindlimb of lorises were reported at between 0.5–1 × BW (Demes and Jungers, 1989; Ishida et al., 1990), and although the hip joint force might be significantly higher, the values reported here seem unrealistic. The estimated hip reaction forces for Galago, however, seem to fit both with the measured ground reaction forces of 15 × BW (Gunther, 1985) and with details of the mechanics of leaping (Burr et al., 1982). It should be noted that, had the average strain of 279 μstrain from the canine model been used as the reference, the predicted hip joint forces would have been only 8.2% less, and still the same relative to one another in both taxa, thus not leading to any significantly different conclusions.

At this stage, we can only speculate about the cause for similarities in strain across the two individuals and the unexpectedly high hip reaction force values in this Loris individual. In the context of understanding both the relevance of the model re-
TABLE 1. Principal strain \( (\varepsilon_{VoI}) \) and Von Mises stress \( (\sigma_{VoI}) \) for each of five loadcases for Galago and Loris models

<table>
<thead>
<tr>
<th>Angle (°)</th>
<th>5 × BW Mean</th>
<th>SD</th>
<th>Scaled Mean</th>
<th>SD</th>
<th>( F_{joint} ) Mean</th>
<th>SD</th>
<th>5 × BW Mean</th>
<th>SD</th>
<th>Scaled Mean</th>
<th>SD</th>
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<td>Galago</td>
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<tr>
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<td>2.57</td>
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1 Calculated joint forces \( (F_{joint}) \) are based on mean strain of 304 \( \mu \)strain.

Fig. 6. a: Calculated \( F_{joint} \) for each loading angle in Galago and Loris. b: Standard deviation \( (|\varepsilon|_{SD}) \) for scaled principal strain at each loading angle. c: Scaled maximum Von Mises stress \( (\sigma_{VoI}) \) for each loading angle. For all graphs, 0° is superior and 90° is anterior.
results for delineating the mechanical significance of trabecular bone structural variation and the utility of finite element modeling in comparative anatomy, there are several simplifications and limitations to the current study that should be discussed. The current study as well as the ongoing work by Strait and colleagues (Strait et al., 2003) highlight some of the methodological and theoretical factors to be considered when attempting to incorporate traditional and micromechanical finite element analyses into comparative anatomical studies. Methodological considerations include model validation, sample size, loading and boundary conditions, material properties, as well as various modeling issues such as element size, shape, and number. Some of these issues have been discussed in relation to the canine model of van Rietbergen et al. (1999) and will be covered further here for the current models.

Of prime importance in relating the results of the Loris and Galago models to the functional morphology of the primate proximal femur is the fact that these results were not validated with empirically-determined strain values from these or similar specimens. It is unknown, therefore, whether these results approximate the true in vivo strain environment in these individuals and, given the simplified boundary and loading conditions and material properties, it is possible that the calculated strain values from these models do not exactly approximate in vivo strain. In their μFE models of the canine proximal femur during the stance phase of walking, van Rietbergen et al. (1999) found higher strain values than those calculated in vivo by Page et al. (1993), suggesting that at least the input loading conditions in the model were somewhat too high.

One issue when using μFE models to estimate tissue-level strains in trabecular bone is that presently μFE is the only technique available to calculate stresses/strains at the trabecular level. Several studies, though, have investigated apparent level properties of trabecular bone cubes and found a close correspondence between empirically-determined elastic properties of trabecular bone (i.e., those calculated using traditional mechanical compression tests) and those predicted by μFE models (Ladd and Kinney, 1998; Kabel et al., 1999b; Niebur et al., 2000). Additionally, Pistoia et al. (2002) used experimental compression testing and μFE models of the distal radius from 54 individuals to demonstrate that μFE models can accurately predict failure loads using uniform isotropic linear elastic material properties. Further validation studies of whole bone fem-

Fig. 7. Histograms of $\epsilon_{\text{VOI}}$ scaled based on estimated joint force ($F_{\text{joint}}$) for (a) 0°, (b) 30°, (c) 60°, and (d) 90° load cases for Galago and Loris models.
oral models could be conducted by comparing predicted external cortical bone strains with those measured from in vivo strain gauges.

Another issue confronting researchers using FE for comparative studies is that of sample size. In this study only one individual per taxon was modeled, greatly limiting the functional conclusions that can be drawn. Further work with more Galago and Loris individuals and other taxa will provide a more distinct picture of the relationship between interspecific trabecular bone architectural variation and locomotor loading. Although a certain trade-off exists between detailed models and sample size, more taxa and more individuals encompassing larger body sizes and larger skeletal elements are clearly important avenues to explore in future modeling projects. The work of Pistoia et al. (2002) is an excellent example of a μ-EF analysis using a large sample (54 human cadaveric specimens) and demonstrates the potential for this method in comparative anatomical studies. The models constructed in the current study, with approximately two million elements, required about 20 hours (clock time) each to solve, while the larger canine and human models of van Rietbergen et al. 1999; 2003 required 30 hours (7.3 million elements) and six weeks (96 million elements), respectively, all on supercomputers. So although time-consuming, large models can be constructed and solved with appropriate computational resources.

The loading conditions used in this study represent another set of simplifications which ultimately affects the results. The simplified loading conditions were driven mainly by the lack of knowledge about the magnitudes and orientations of the loads at the hip joint during locomotion in either of these animals. Joint forces during locomotion are the resultant of muscle forces and gravitational forces and cannot be estimated or simulated based solely on the angle between the trunk and femur as was done here. The force magnitude of five times body weight that was used was based on published measurements of hip joint forces in humans and other animals (Bassey et al., 1997; Bergmann et al., 1984, 1993, 1999; Page et al., 1993). The assumption was that five times body weight is a decent approximation of the potential maximum forces generated in the femoral head during normal or controlled locomotor activity in a hindlimb-dominant animal. Additionally, the actions of muscles were not specifically modeled, but to some extent their effects were included, since the estimate of joint forces used to load the femur was based on reports of measured hip joint forces which include the effects of muscles. Certainly one important improvement to the current models would be to add more detailed joint loading information, including specific joint reaction and muscle forces, and to apply these loads across a more evenly distributed surface to simulate an acetabular cup, rather than using the two discrete loading platforms. Models of other taxa (e.g., humans) may benefit from the detailed work of Bergmann and colleagues (Bergmann et al., 1984; Bergmann et al., 1993; Bergmann et al., 1995; Bergmann et al., 1999) using instrumented prostheses, but unfortunately for non-human primate studies, we currently may not be able to model joint forces accurately.

In the models in this study, uniform isotropic material properties were applied to both cortical and trabecular bone. The use of isotropic material properties facilitates solution of the models but also may affect the results. Cortical bone may be most appropriately modeled as transversely isotropic or orthotropic each requiring more elastic constants (Young’s moduli, Poisson’s ratios, and shear modulus) than used here (Beaupre and Carter, 1992). Using these properties rather than isotropic properties would likely produce significantly different results in cortical bone strains depending on the directionality of the external loads. For trabecular bone, however, although the actual material is anisotropic, it has been shown that the elastic properties can be almost entirely characterized by the three-dimensional fabric architecture and that an isotropic tissue modulus is an effective model (Kabel et al., 1999b). The close relationship between the elastic and fabric principal directions in trabecular bone structures (Odgaard et al., 1997; Kabel et al., 1999b) demonstrates that, although the trabecular bone material itself is either orthotropic or transversely isotropic, the behavior of the trabecular structure is effectively isotropic. There is, therefore, little error in assuming isotropy at the trabecular bone tissue level and the values of these material properties are likely to be relatively homogeneous across anatomical sites (Cowin, 1997). The use of uniform isotropic material properties across the trabeculae within these models is therefore justified.

The actual value for the Young’s modulus of trabecular bone is quite variable depending on anatomical location (Goldstein et al., 1983; Goldstein, 1987), but it is certainly different from that of cortical bone (Choi et al., 1990). So it is possible that the trabeculae in the current models are either too stiff (Young’s modulus too high for trabecular bone) or that the cortical bone is not stiff enough (Young’s modulus too low for cortical bone) due to the uniform material properties assignment. In addition, the material properties research is based entirely on human and other large mammal datasets. Nothing is known of the material properties of either bone type in these small-bodied strepsirrhines. One positive result of the uniform assignment of material properties for both bone types in both species is the effective removal of the effect of this model parameter as a factor influencing the results and the interpretation of the models. The interpretation of the results from a comparative anatomic point of view is thereby simplified. From a more practical perspective, it would not be easy to implement material properties other than isotropic in cortical bone structures since this would require knowledge about the
orthotropic elastic constants which are not well known. Additionally, the $\mu$FE code assumes isotropic properties in order to utilize the fast iterative solver which facilitates solution of these large-scale models, so modeling cortical bone as anything but isotropic is not possible using the current methodology. One improvement to the current models and in future modeling efforts would be to set different material properties for cortical and trabecular bone to more closely mimic the actual material properties of bone.

In addition to the effects of the various input parameters on the models, the FE and $\mu$FE methods also introduce some potential issues for comparative studies. The voxel modeling approach, based as it is on the CT scan datasets, produces hexahedral brick elements with jagged edges rather than smoothed continuous surfaces such as produced by tetrahedral or other elements. Such a modeling approach has been linked to errors in the calculations of stress and strain, especially at bone surfaces (Gundersen and Jensen, 1985; Jacobs et al., 1993; van Rietbergen et al., 1996b; Camacho et al., 1997). Errors in the calculation of the histograms, however, have been found to be less than seven percent (van Rietbergen et al., 1996b) and these errors may be concentrated in areas of low stress anyway (Guldberg and Hollister, 1994). The results reported here may have some slight inaccuracies as a result of the jagged edges of the models, but the overall comparison between the models remains valid and useful. The value that such modeling offers (i.e., high-resolution tissue-level models) and the fact that this high resolution is typically not possible with traditional FE modeling outweighs the potential inaccuracies of the calculations.

The voxel modeling approach is a useful technique to construct large-scale, geometrically accurate models of trabecular and whole bone anatomy. Hexahedral brick elements are capable of effectively modeling compression, tension, and shear deformations, but may be slightly deficient in representing bending since they may be too stiff. For the purpose of modeling trabeculae, this drawback is not a problem because the individual trabeculae are loaded in compression and tension. In modeling the function of the femoral head and neck in primates, however, these modeling limitations may be more critical especially in models of neck function in anthropoids.

In addition to the methodological issues presented by the FEM itself, the use of FEM in comparative analyses also may raise some potential problems. In comparative studies, larger sample sizes spanning a range of body sizes are clearly an important goal to ensure robust functional analyses. In modeling animals and skeletal elements of different sizes, several issues may arise. In the current study, because the specimens were of similar size, the high-resolution CT scan data and the consequent voxel and element sizes were the same. For larger individuals, however, the scan resolutions and element sizes may be significantly lower and the number of elements will be greater. An obvious modeling goal is to have multiple elements spanning a single trabecular strut as in the current study with approximately four or more elements per single trabecular strut. In larger animals this goal may not be attainable and the ability to accurately model trabecular structures will be reduced. Ulrich et al. (1998) found a significant reduction in the accuracy of model results with resolutions greater than about 80 $\mu$m which also generally corresponds to the upper resolution at which trabecular structures can be accurately quantified (Kothari et al., 1998). They also found that these resolution dependencies can vary across specimens as a function of the trabecular thickness (Ulrich et al., 1998). The use of $\mu$FE in comparative analyses, therefore, may be limited to taxa and skeletal elements small enough to be imaged with voxel resolutions less than 80 $\mu$m and models should be evaluated on a case-by-case basis.

**CONCLUSIONS**

The $\mu$FE models constructed in the current study provide an initial mapping of the tissue-level strains in the femoral head and neck trabecular bone of *Galago* and *Loris*. The models very accurately represent the geometry of the proximal femur of these two individuals and, despite the various simplifications and limitations, provide some interesting, albeit preliminary, insights into the functional morphology of the proximal femur as well as the mechanical behavior of trabecular bone in the femoral head of these two primates. The fact that the structural differences between these two individuals is not also reflected in differences in the distribution or magnitudes of stress and strain through the femoral head as modeled here raises the question of whether trabecular bone structural variation is related to locomotor behavioral differences and consequently whether it is a functionally-relevant characteristic. The mechanical relevance of trabecular structure has been clearly demonstrated in studies showing the correlation between the fabric structure and the mechanical elastic properties (Kabel et al., 1999a; Kabel et al., 1999b; Kabel et al., 1999c; Ulrich et al., 1999), the close relationship between the fabric and elastic principal directions (Odgaard et al., 1997), and the role of external loading and disuse on the development and loss of trabecular bone (Biewener et al., 1996). The limited results here suggest that the relationship to locomotor behavior may be a complex one and that all of the observed interspecific structural variation may not be mechanically relevant or driven solely by differences in the loading environment. It could also be the case, however, that mechanical differences would emerge between these taxa with larger taxonomic sample sizes as well as a broader range of load orientations, especially in the mediolateral dimension, which might more realistically approximate the actual loading conditions at the hip joint.
The models in the current study neither validate nor invalidate the functional significance of trabecular bone structural differences in strepsirrhines and the potential relevance to locomotor behavioral differences, but they do suggest that simplistic assumptions about a tight correlation between locomotor forces and trabecular bone structure in these animals may not be entirely valid. Additionally, because there are precious little data concerning locomotor mechanics and kinematics in lorises and galagos, our understanding of hip joint and hindlimb function in these animals is limited. Further kinematic and biomechanical modeling of the hindlimb of strepsirrhine primates during various behaviors will greatly improve our understanding of the inter-relationships among joint function, locomotion, and bone structure. A better delineation of the mechanical significance of variation in trabecular bone structure as well as the estimation of hip joint forces across different primates will ultimately lead to a better understanding of the adaptive significance of bone form. Within evolutionary morphological studies, quantification of trabecular structure together with μFE models to estimate tissue-level strains and hip joint forces represent powerful analytic tools for the interpretation and reconstruction of locomotor and positional behavior in extinct animals (Ryan and Ketcham, 2002a). Many factors must be considered in using finite element methods in comparative anatomical studies including issues of model validation, material properties, loading and boundary conditions, and sample size. The models presented here provide an initial assessment of trabecular structural adaptations and demonstrate the potential of finite element models while at the same time pointing to directions for further investigation. Continued work with more individuals and more detailed and refined models will greatly improve our understanding of the relationship between bone structure and external loading.

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LITERATURE CITED


FE ANALYSIS OF PRIMATE TRABECULAR BONE


