

Calcaneal elongation and bone strength in leaping galagids

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Abstract

Objectives: Small-bodied vertical clinging and leaping primates have elongated calcanei which enhance leap performance by optimizing leap velocity, distance, and acceleration, but at the expense of experiencing relatively large forces during takeoff and landing. This study tests the hypothesis that the elongated calcaneus of leaping galagids is adapted to resist larger and more stereotyped bending loads compared to more quadrupedal galagids.

Materials and Methods: The calcanei of 14 individuals of *Otolemur* and 14 individuals of *Galago* (three species of each genus) were μ CT scanned. Calcaneal cross-sectional properties (maximum and minimum second moments of area and polar section modulus) were obtained from a slice representing the 50% position of bone segment length and dimensionless ratios were created for each variable using calcaneal cuboid facet area as a proxy for body mass.

Results: There were no significant differences in size-adjusted bending strength between *Galago* and *Otolemur*. *Galago* exhibited more elliptically shaped calcaneal cross sections, however, suggesting that its calcanei are more adapted to stereotyped loading regimes than those of *Otolemur*.

Discussion: The results suggest that the calcaneus of specialized leapers is adapted to more stereotyped loading patterns. The lack of predicted bone strength differences between *Galago* and *Otolemur* may be related to body size differences between these taxa, or it may indicate that loads encountered by *Galago* during naturalistic leaping are not reflected in the available experimental force data.

KEYWORDS

ankle, cross-sectional geometry, leaping, locomotion, primate

1 | INTRODUCTION

Saltatorial locomotor behaviors (i.e., leaping and hopping) are used by many mammals to facilitate maneuvering through three-dimensional (3D) discontinuous uneven habitats, and serve important functions like predator avoidance and hunting for prey. Leaping is an especially crucial behavior for many extant primates and is hypothesized to have been vital to the evolution of Order Primates body plans during the Paleocene-Eocene transition (e.g., Crompton, 1995; Szalay, 2007; Szalay & Dagosto, 1988). A suite of external morphological features in

the hindlimb skeleton has been functionally related to leaping (e.g., Dagosto, 2007; Fleagle, 2013; Runestad Connour, Glander, & Vincent, 2000). A particularly striking character is calcaneal elongation, which occurs in small-bodied specialized leapers such as *Galago senegalensis*, where the calcaneus is relatively long compared to sister taxa that leap less frequently like *Otolemur crassicaudatus* (e.g., Boyer, Seiffert, Gladman, & Bloch, 2013; Gebo, 1987, 1989; Hall-Craggs, 1966).

Among galagids, relative tarsal length is correlated with leaping prevalence, and species that spend more time vertical clinging and leaping (VCL) have relatively longer tarsals than those spending more

time using quadrupedal forms of locomotion (Boyer et al., 2013; Gebo, 1987, 1989; Hall-Craggs, 1965; Jouffroy & Lessertisseur, 1979). Elongated tarsals increase functional hindlimb length, which allows for an increase in the distance over which takeoff forces can be generated during hindlimb extension (e.g., Peters & Preuschoft, 1984). This ultimately contributes to increasing leap velocity, which, along with greater acceleration, is critical to efficiently achieve a given leap height and distance. In addition to limb elongation, leap acceleration can also be maximized by decreasing overall distal hindlimb mass (e.g., Peters & Preuschoft, 1984).

Primate vertical clingers and leapers also generate tremendous forces during takeoff and landing that are orders of magnitude larger than those experienced during typical primate quadrupedal locomotion. Most arboreal and terrestrial quadrupeds experience peak hindlimb substrate reaction forces that are ~50–100% of body weight during high speed behaviors (e.g., running, galloping; Hanna, Polk, & Schmitt, 2006; Schmitt & Hanna, 2004). In a sample of lemurs, platyrrhines, and cercopithecines, Granatosky, Fitzsimons, Zeininger, and Schmitt (2018) report average impulses (i.e., the integral of force over time) during quadrupedal walking on a pole that are 5–42% of body weight per second. In contrast, during leaping, medium- to large-bodied vertical clingers and leapers experience forces ~500–1,400% of body weight (Demes, Fleagle, & Jungers, 1999), which are significantly higher in magnitude compared to when these same animals walk quadrupedally (Granatosky, Tripp, Fabre, & Schmitt, 2016). Furthermore, *Galago senegalensis* experiences peak forces during the takeoff phase of vertical leaping that are ~1,500% of body weight (Aerts, 1998). These relatively larger forces likely engender larger loads on limb bones, which would need to be resisted, in part, by the distribution of cortical bone within the diaphysis. Measures of cortical bone structure are typically assessed from midshaft cross-sectional geometry, where measures of moment of inertia (I , an estimate of bending strength), the ratio of maximum and minimum moments of inertia (I_{max}/I_{min} , a reflection of cross-sectional shape from circular to elliptical), polar section modulus (Z_p , proportional to twice bending strength), polar second moment of area (J , an estimate of torsional strength), and cortical area ($Ct.Ar$, a quantification of bone mass and estimator of compressive strength), are used to make inferences about bone functional adaptation to behavior (Ruff, Holt, & Trinkaus, 2006).

Previous studies have shown that femoral cross-sectional geometry can distinguish between primates that habitually leap frequently from those that leap less frequently. In leaping galagids, the femur shows larger I values in the anteroposterior direction (I_{AP}) relative to the mediolateral direction (I_{ML}), which suggests that it has the greatest resistance to bending in the anteroposterior plane (Burr, Piotrowski, Martin, & Cook, 1982; Demes & Jungers, 1993; Terranova, 1995). In contrast, more quadrupedal galagids show more similar femoral I_{AP} and I_{ML} values, indicating similar resistance to bending in the anteroposterior and mediolateral directions, or more multidirectional loading irrespective of any specific axis (Terranova, 1995). Furthermore, while femoral midshaft $Ct.Ar$ is greater than humeral midshaft $Ct.Ar$ in all galagids, this inter-limb difference (i.e., forelimb-hindlimb

asymmetry) is more pronounced in leaping species (Demes & Jungers, 1993; Terranova, 1995). These data therefore suggest that in leaping galagos, the hindlimb (i.e., femur) is relatively stronger than in quadrupedal galagos to resist increased locomotor loads as discussed above. These data are also corroborated by studies on lemur and platyrrhine leapers, which show relatively greater J and $Ct.Ar$ values among leaping-prevalent species (Runestad Connour et al., 2000).

Whether differences exist in strength properties in proximal tarsal bones like the elongated calcaneus among species that differ in leaping prevalence remains unknown. This is because the only foot bones of nonhuman primates in which cross-sectional geometry has been studied are metatarsals, wherein predictable relationships between strength properties and locomotion have been found in apes and monkeys (e.g., Marchi, 2005, 2010; Patel et al., 2018; Patel, Organ, Jashashvili, Bui, & Dunsworth, 2018). Although the calcaneus is frequently modeled as a beam in ungulates (e.g., Keenan, Mears, & Skedros, 2017; Skedros, Su, Knight, Bloebaum, & Bachus, 2019; Su, Skedros, Bachus, & Bloebaum, 1999), this method has yet to be applied to the distally elongated calcaneus of galagids, which resembles a long bone in both external morphology and in cross section (Hall-Craggs, 1966).

Despite the benefits of calcaneal elongation on hindlimb kinematic performance, there may be negative consequences to having absolutely longer tarsals. Because the hindlimb experiences larger substrate reaction forces during leaping (both in takeoff and landing) than during quadrupedalism (Demes et al., 1999), the elongated calcaneus of habitual leapers could potentially be subjected to more frequent and higher magnitudes of bending and torsion, either from substrate reaction forces or from muscle forces. For example, *m. triceps surae*, which attaches to the calcaneal tuber and likely applies a bending load to the distal part of the tarsus and metatarsus while the foot is in contact with the substrate, has been estimated to produce ~100–150 N of force during takeoff for a vertical leap in *Galago senegalensis* with a body mass of just ~2.5 N (Aerts, 1998). If this hypothesis is correct, the elongated calcanei of specialized leaping primates should be relatively stronger in bending compared to sister taxa that leap less frequently to attenuate these more stressful load regimes.

The objective of this study is to identify cortical bone adaptations to leaping in the distal calcaneus in closely related extant galagid primates. We use a narrow phylogeny approach to test the hypothesis that in galagid taxa that habitually leap more frequently, the calcaneus will be adapted to resist greater bending and torsional loads and will demonstrate more elliptical cross sections indicative of stereotyped loading patterns compared to those of species that leap less often. Small-bodied galagids are an ideal group within which to test this hypothesis because these taxa exhibit variation both in the amount of time spent leaping versus quadrupedal and in degree of elongation of hindlimb segments. Among galagos, the most specialized leapers are the lesser galagos (e.g., *Galago senegalensis* and *G. moholi*, Nash, Bearder, & Olson, 1989), which use VCL locomotion and habitually leap 50–60% of the time (Gebo, 1988; Jouffroy & Günther, 1985). Other galagid taxa also engage in leaping, but do

not specialize in VCL locomotion; the most quadrupedal species are the greater galagos (*Otolemur*) that leap only ~20% of the time (Crompton, 1984), and are often more habitually quadrupedal (e.g., Charles-Dominique, 1977; Crompton, 1984; Nash et al., 1989; Walker, 1979). This overall behavioral difference between *Otolemur* and *Galago* is reflected in their relative calcaneal lengths where *Galago* has relatively longer calcanei (Boyer et al., 2013; Gebo, 1988).

2 | METHODS

2.1 | Sample

The sample (Table 1) consists of calcanei from three *Galago* species that are frequent specialized leapers (*G. gallarum*, *G. moholi*, *G. senegalensis*) and from three *Otolemur* species that leap less frequently and do not use specialized forms of leaping (*O. crassicaudatus*, *O. garnettii*, and *O. monteiri*). Samples were restricted to adult, non-pathological specimens (as determined by complete or near-complete epiphyseal fusion of the tibia). Right side bones were chosen, but when unavailable, left side elements were used and digitally mirror-imaged prior to analyses. All but four specimens were borrowed from the collections of the American Museum of Natural History (New York, NY); these calcanei were μ CT scanned at the Molecular Imaging Center at the Keck School of Medicine of USC (Los Angeles, CA) using a SCANCO μ CT 50 specimen scanner with 90 kV and 200 μ A energy settings and 14 μ m voxel resolution (except for one specimen that was scanned at 20 μ m resolution). μ CT scans of the remaining four calcanei were downloaded from MorphoSource.org, which were scanned using a Nikon XTH 225 ST scanner with 25–40 μ m resolution. All raw scans were saved in either 16-bit DICOM or TIFF format.

2.2 | Cortical bone properties

Each calcaneus was virtually reoriented using Avizo Lite v. 9.3 or 9.5 software (Thermo Fisher Scientific) according to its anatomical axes, and if necessary, was digitally mirror-imaged to reflect a right-side element (Figure 1). First the Align Principal Axes module was applied to a 3D surface model of the data; this module orients the model according to its three principal axes and results in alignment that is close to proper anatomical position and requires only minor adjustments thereafter from the user. The model was then manually adjusted using the Transform Editor such that the calcaneal tuber was oriented superiorly, the astragalar articular facets oriented ventrally, and the sustentacular facet oriented medially (Figure 1). The long axis of the calcaneal distal segment was oriented vertically such that its cross sections would be oriented orthogonal to the long axis of the bone (i.e., sections in the XY plane were oriented transversely). The reoriented surface model was converted to a volumetric model using the Scan Surface to Volume module; this module voxelizes the data such that it can be resliced as if it were a solid object. In order to identify the “midshaft” of the distal calcaneus, two slices were placed to delineate the proximal and distal articular boundaries of the calcaneal distal segment (Figure 2). The proximal slice was manually placed at the distal-most extent of the sustentacular facet, while the distal slice was placed at the proximal extent of the tuberosity for the navicular articulation. A third slice was then placed at 50% the distance between the proximal and distal calcaneal slices which represents the midshaft of this interarticular calcaneal distal segment length (Figure 2). We analyze the midshaft of the distal calcaneus in an effort to characterize overall calcaneal strength (reviewed in Ruff, 2008). The midshaft slice was then exported as a binarized DICOM image for subsequent cross-sectional geometry analysis.

Following previous researchers (Byron, Herrel, Pauwels, Muynck, & Patel, 2015; Lewton, Ritzman, Copes, Garland, & Capellini,

TABLE 1 Sample size and locomotor classification for each species

Genus	Species	Species mean body mass ^a	Relative distal calcaneal elongation (DL/TL) ^b	% Leap ^c	Locomotor category	Locomotion reference	Source ^d	Male	Female	Unknown	Total N
<i>Galago</i>											14
	<i>gallarum</i>	0.200	0.715	–	VCL	Nash et al., 1989	AMNH	1	0	0	1
	<i>moholi</i>	0.180	0.690	53%	VCL	Jouffroy & Günther, 1985	AMNH & MS	1	5	2	8
	<i>senegalensis</i>	0.283	0.700	63%	VCL	Gebo, 1988	AMNH	2	0	3	5
<i>Otolemur</i>											14
	<i>crassicaudatus</i>	1.150	0.599	~22%	AQ	Crompton, 1984	AMNH	6	2	2	10
	<i>garnettii</i>	0.764	0.610	–	AQ	Nash et al., 1989	MS	0	0	2	2
	<i>monteiri</i>	1.150	0.598	–	AQ	Nash et al., 1989	AMNH	1	0	1	2

^aSmith and Jungers (1997).

^bDL/TL, distal calcaneal length/total calcaneal length. DL is measured to the calcaneal cuboid facet.

^cPercentage of travel via leaping locomotion. “–” denotes missing data.

^dAMNH, American Museum of Natural History; MS, MorphoSource.

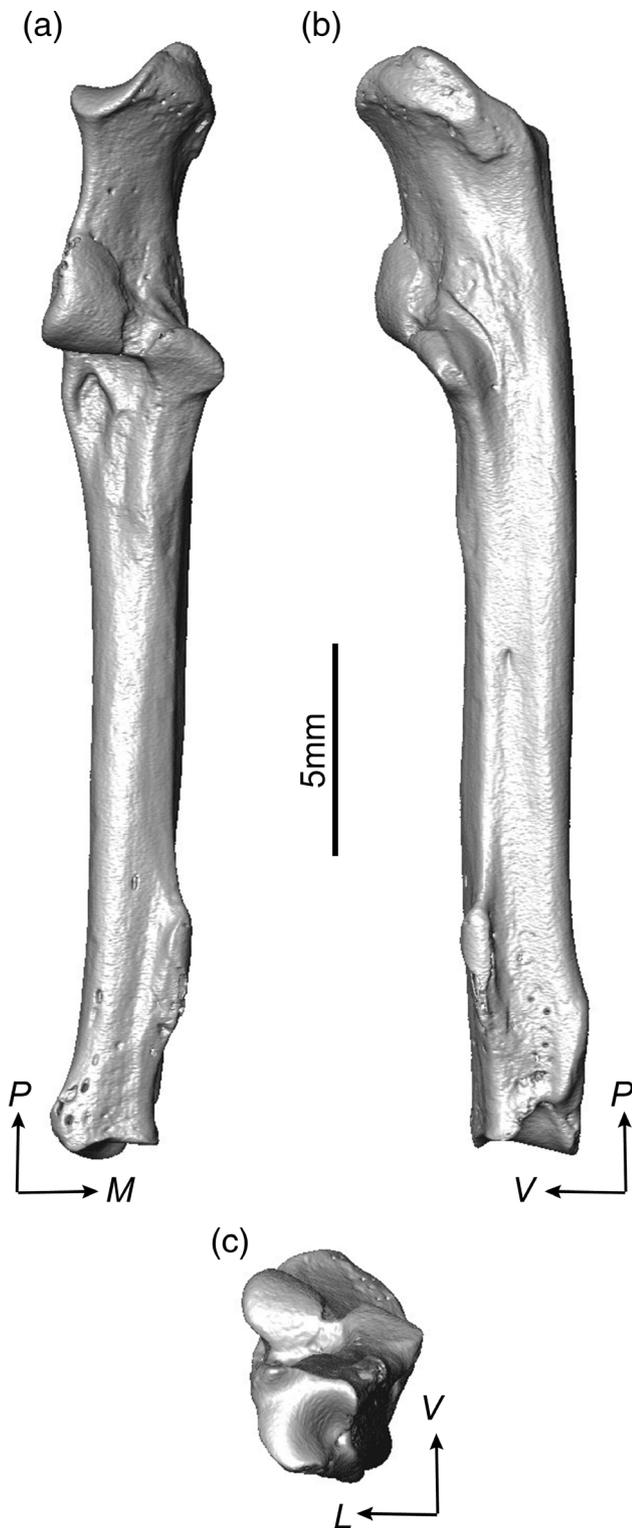


FIGURE 1 Virtual reconstruction of a *Galago senegalensis* (AMNH 35445) calcaneus depicting the anatomical orientations used in this study. The calcaneus is shown in (a) ventral, (b) medial, and (c) distal views. The abbreviations for arrow directions are: P, proximal; M, medial; V, ventral; D, dorsal; L, lateral. The scale bar represents 5 mm. The specimen shown here is available on www.morphosource.org

2019; Patel, Jashashvili, et al., 2018; Patel, Organ, et al., 2018), cross-sectional properties were calculated using the SliceGeometry protocol

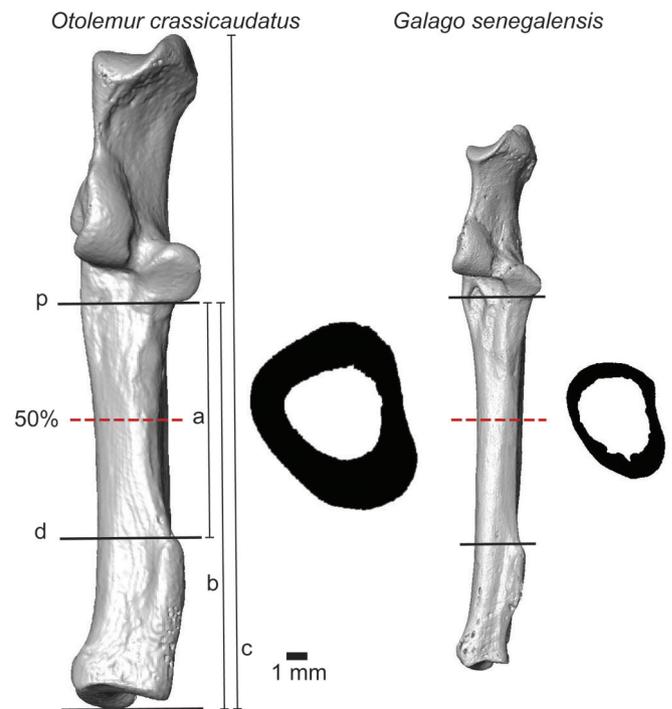


FIGURE 2 Representative models of *Otolemur* (left) and *Galago* (right) calcanei. Cross-sectional properties were determined at the 50% slice location (indicated by the red dotted lines) between the proximal (p) and distal (d) articulations (with the astragalus and navicular, respectively; indicated by solid black horizontal lines). Calcaneal interarticular segment length (a) was determined from the region between p and d. Total calcaneal distal segment length (b) was determined from p to the distal-most extent of the calcaneal cuboid facet. Total calcaneal bone length (c) was determined from the proximal-most extent of the calcaneal tuber to the distal-most extent of the calcaneal cuboid facet

with default thresholding settings in the BoneJ plugin (Doube et al., 2010) implemented in ImageJ software (Schneider, Rasband, & Eliceiri, 2012). The following cross-sectional properties were calculated: maximum and minimum second moments of area (I_{max} and I_{min}) and polar section modulus (Z_p). To account for size differences in the comparative sample (and following Cosman, Sparrow, & Rolian, 2016; see also Polk et al., 2000; Ruff, 2000), dimensionless ratios were created using bone length and body mass. Total calcaneal bone length and total calcaneal distal segment length were also measured virtually in Avizo Lite using bounding box dimensions; total calcaneal distal segment length was measured from the medial astragalus facet to the most distal projection of the cuboid facet (Figure 2). Calcaneal cuboid facet area (CCFA) was used as a proxy for body mass, as Yapuncich, Gladman, and Boyer (2015) found this measure to be strongly significantly correlated with body mass. To quantify CCFA, the articular surface for the calcaneal cuboid facet was first isolated from surface models in Avizo Lite, and then subsequently exported to Geomagic Wrap software (v. 2015, 3D Systems, Inc.) in which it was cleaned (e.g., smoothed of spikes and holes filled) and measured. $ScZ_p = Z_p$ divided by the product of CCFA and bone segment length. Cross-sectional shape was examined by the ratio of I_{max} and I_{min} , with values

that deviate more from 1.0 representing more elliptical-shaped cross sections.

2.3 | Analytical methods

Given the differences in body size and calcaneal elongation between *Galago* and *Otolemur* (e.g., Boyer et al., 2013), the relationships between calcaneal distal segment length, CCFA, and cross-sectional properties were investigated using least squares regression on natural log (ln) transformed data. To test the hypothesis that differences in bone strength properties are due to differences by locomotor category, one-tailed *t*-tests were performed on scaled cross-sectional properties. If more frequent leapers (i.e., *Galago*) demonstrate significantly larger values for ScZ_p and more elliptical bone cross sections (i.e., larger I_{max}/I_{min} values), then our predictions will be supported. Statistical analyses were performed in JMP Pro v.14 (SAS Institute Inc.).

3 | RESULTS

Species means and standard deviations for raw values of segment length, CCFA, Z_p , I_{max} , and I_{min} , as well as ScZ_p and I_{max}/I_{min} are in Table 2, and Table S1 includes data for these variables for each individual. Across the entire sample, calcaneal segment length is significantly correlated with cross-sectional properties at midshaft of the interarticular calcaneal segment (Table 3). Examining this relationship within genera reveals a statistically significant positive correlation between calcaneal segment length and cross-sectional properties in *Galago*, but not in *Otolemur* (Table 3). Similarly, CCFA is significantly positively correlated with Z_p in the entire sample ($r = .96$, $p < .0001$) and within *Galago* ($r = .82$, $p = .0004$), but not within *Otolemur*.

The *t*-tests demonstrate that ScZ_p does not significantly differ according to taxon/locomotor behavior (1-tailed $p = .95$). A boxplot of these data show more variability within the *Otolemur* sample compared to the *Galago* sample (Figure 3a, see also Table 2).

TABLE 2 Summary statistics (mean and SD) of raw and scaled values of calcaneal cross-sectional properties, calcaneal cuboid facet area (CCFA), and calcaneal distal segment length

Taxon	CCFA (mm ²)		Calcaneal distal segment length (mm)		Z_p (mm ³)		ScZ_p		I_{max} (mm ⁴)		I_{min} (mm ⁴)		I_{max}/I_{min}	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Galago</i> generic mean	5.27	1.29	19.50	1.51	1.93	0.37	0.019	0.003	1.90	0.50	0.88	0.20	2.17	0.25
<i>Galago gallarum</i>	5.95		22.39		2.15		0.016		1.97		1.06		1.86	
<i>Galago moholi</i>	5.05	0.65	19.05	0.48	1.99	0.26	0.021	0.002	1.99	0.26	0.89	0.18	2.27	0.20
<i>Galago senegalensis</i>	5.47	2.10	19.65	2.12	1.79	0.53	0.017	0.003	1.74	0.80	0.82	0.26	2.08	0.28
<i>Otolemur</i> generic mean	18.67	2.91	20.77	0.76	8.78	2.77	0.023	0.010	13.14	5.92	7.48	2.87	1.73	0.24
<i>Otolemur crassicaudatus</i>	17.57	2.41	20.46	0.41	8.14	2.59	0.023	0.010	11.64	5.50	6.88	2.74	1.67	0.19
<i>Otolemur garnettii</i>	21.00	3.85	20.97	0.19	8.21	2.47	0.019	0.010	13.17	6.87	6.56	1.89	1.94	0.49
<i>Otolemur monteiri</i>	21.80	0.67	22.08	1.20	12.56	0.26	0.026	0.003	20.59	1.44	11.40	0.08	1.81	0.14

TABLE 3 Correlations and *p*-values for the relationships between ln-transformed polar section modulus (Z_p) and calcaneal segment length and CCFA using least squares regression on the sample of individuals

	ln segment length		ln CCFA	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
Total sample	.61	.0006	.96	<.0001
<i>Otolemur</i>	.50	.0657	.40	.1584
<i>Galago</i>	.58	.0309	.82	.0004

Note: Bold denotes statistical significance at $\alpha = .05$.

There is a significant difference in calcaneal cross-sectional shape (I_{max}/I_{min}) between taxa, with *Galago* having more elliptically-shaped bones (1-tailed $p < .0001$, Figure 3b).

4 | DISCUSSION

Strepsirrhine primates experience higher forces on their hindlimbs when leaping relative to when adopting pronograde quadrupedal locomotion (Demes et al., 1999; Granatosky et al., 2016). Because leaping primates have relatively longer femora, these bones tend to be relatively stronger to help resist larger bending moments, and this is reflected by their midshaft cross-sectional geometry (Burr et al., 1982; Demes & Jungers, 1993; Terranova, 1995). Leaping galagids also have relatively longer calcanei, and thus it is likely that the calcanei would also be adapted to resist the higher forces that are encountered during leaping. In this study, we used a narrow phylogeny approach to identify form-function relationships between calcaneus cortical bone structure and locomotor behavior in galagids. Specifically, we compared three species of vertical clinging and leaping *Galago* with three species of *Otolemur* which are primarily quadrupedal. We predicted that *Galago*, which leaps more frequently (observed up to 63% of locomotor bouts [Gebo, 1988]) would have

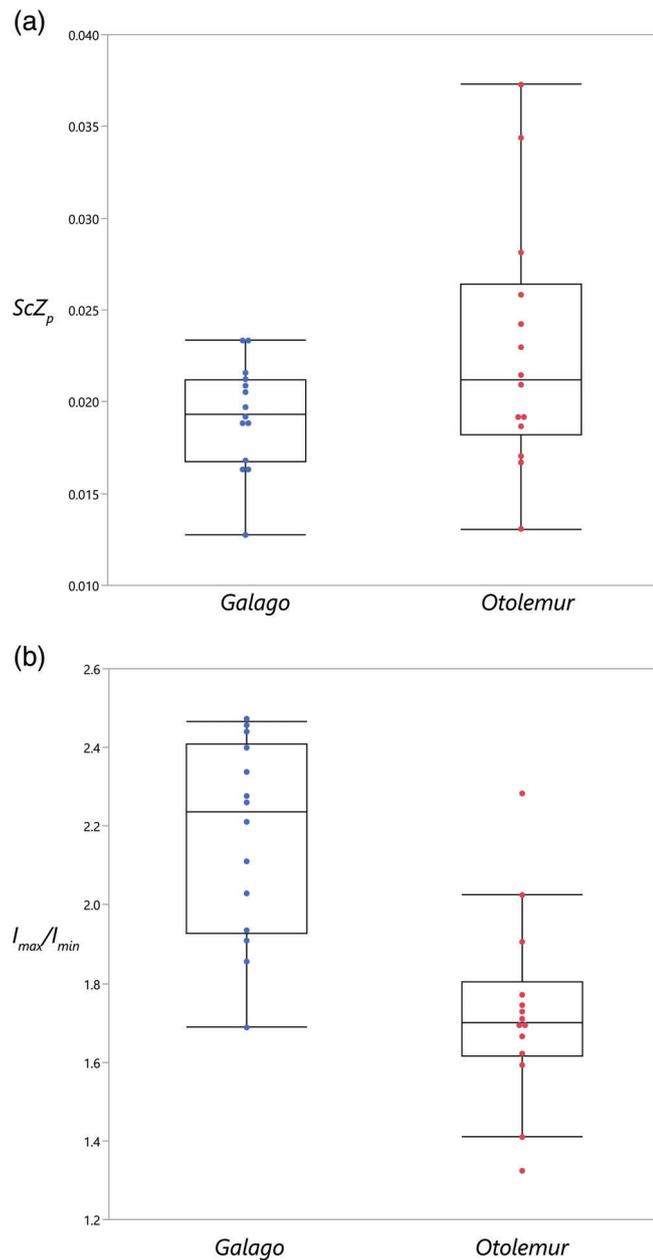


FIGURE 3 Boxplots by taxon for scaled polar section modulus (ScZ_p , a) and the ratio of I_{max}/I_{min} (b). Horizontal lines within each box illustrate the sample median. Boxes envelop the inter-quartile range of the sample distribution, and whiskers encompass the range excluding outliers. Filled circles beyond whiskers indicate outliers. Blue filled circles denote vertical clinging and leaping *Galago*, red filled circles denote the more quadrupedal *Otolemur*. Larger values of I_{max}/I_{min} indicate more elliptical cross sections

calcanei structurally adapted to resist greater bending stresses compared to *Otolemur*, which leaps less frequently (up to perhaps 22% of locomotor bouts [Crompton, 1984]). Additionally, we predicted that *Galago* would have more elliptical calcaneal cross sections as a result of more stereotyped loading regimes (i.e., single-plane loading). Overall, results of this comparative study did not identify locomotor differences in size-adjusted values of bending strength (ScZ_p) between these genera. However, our hypothesis that *Galago* would have more

elliptical calcaneal cross sections than *Otolemur* (as indicated by larger I_{max}/I_{min} ratios) was supported.

The absence of significant differences in this study in calcaneal strength properties may, in fact, reflect biological similarity of the postcranial skeletal anatomy of these two genera, perhaps suggesting that soft tissues of the musculoskeletal system modulate calcaneal bone strains. However, it is also possible that comparisons at the genus level as performed here obscure potential species-level variation that may be related to differences in locomotor behaviors resulting from localized variation in habitats and ecologies. Unfortunately, leaping data from wild animals or even laboratory animals from a broad range of galagid species are sparse, further making species-level comparisons difficult. However, incorporating non-galagid taxa of small, specialized and non-specialized leapers, such as tarsiers and cheirogaleids, which are closer to the size of *Galago* species and also have elongated distal calcanei (Boyer et al., 2013), could be investigated in the future to validate the observed results. Naturally, more *in vivo* locomotion data from more galagid taxa is also needed and would prove useful.

In addition to the potential effects of sampling, it is possible that the available published experimental data on substrate reaction forces these animals experience during leaping locomotion do not accurately reflect the forces that they encounter in their natural environments. Experimental data demonstrate that quadrupedal strepsirrhines generally experience smaller substrate reaction forces than vertical clinging and leaping strepsirrhines during locomotion (Demes et al., 1999; Demes & Günther, 1989; Granatosky et al., 2016; Günther, Ishida, Kumakura, & Nakano, 1991), however, data on substrate reaction forces in the smaller leaping taxa such as *Galago* are less abundant than those on larger leaping taxa such as *Propithecus*. Another possible confounding factor with experimental force data on leaping is that most studies have recorded leap takeoff and landing forces on horizontal substrates, but not on vertical substrates (but see Demes et al., 1999), and, perhaps most importantly, the forces encountered in small terminal branches that are highly compliant (which, of all substrate types, are least likely to engender larger reaction forces) have not been measured. Thus, the available experimental data may not be adequate to test hypotheses regarding the adaptive relationship between bone morphology and substrate reaction forces encountered during naturalistic VCL locomotion. Future force plate data collected using naturalistic environments for small-bodied leapers should try to include thin, compliant vertical substrates in which loads may be significantly less than those resulting from larger diameter, more rigid arboreal substrates.

An alternative explanation for the lack of bone strength differences between these taxa may be that calcaneal loading—and, importantly, the functionally adaptive response of calcaneal cortical bone to loading regimes—may be more complex than assumed here. Previous work has found that both external and internal bone morphology are generally reflective of the loading regimes to which bone is subjected. For example, external forelimb bone shape and peak locomotor forces significantly co-vary in strepsirrhines (Fabre, Granatosky, Hanna, & Schmitt, 2018), and numerous studies on bone internal morphology

have demonstrated correlations between cortical bone cross-sectional properties and loading regimes (reviewed in Ruff et al., 2006). However, the interpretation of the relationship between bone cross-sectional properties and loading history is only as good as the accuracy of the biomechanical model of bone loading from which morphological predictions derive (Lieberman, Polk, & Demes, 2004). While the calcaneus of white-tailed deer has been modeled as a cantilever beam and validated using experimental data (Su et al., 1999), the calcaneus of galagids is unique in morphology, not resembling most other mammalian calcanei, and as a result, there is currently no validated model of its loading regimes. This could be addressed in the future by experimentally investigating the patterns of bending experienced by the galagid calcaneus using bone strain data, or possibly modeled using *in silico* methods (e.g., finite element analysis).

Our results demonstrated more circular calcaneal cross sections in *Otolemur* and more elliptical cross sections in *Galago*, suggesting that during locomotion, the *Galago* calcaneus experiences more stereotyped loading patterns predominantly confined to a single plane (cf. Carlson, 2005; Patel, Ruff, Simons, & Organ, 2013). Our results also documented more variation in ScZ_p within *Otolemur* (Figure 3a). This variation in bone strength properties adds further support to the hypothesis that *Otolemur* experiences more varied loading regimes as a result of incorporating more quadrupedal behaviors into its locomotor repertoire, resulting in variable foot postures throughout the step cycle and depending on substrate diameter, orientation and compliance. Conversely, the reduced variation observed within species of *Galago* supports the hypothesis that *Galago* encounters more stereotyped calcaneal loading patterns resulting from an emphasis on hindlimb flexion and extension movements in the sagittal plane during VCL behaviors (Hall-Craggs, 1966).

The lack of support for the hypothesis that *Galago* would have relatively stronger calcanei than *Otolemur* raises the question of whether there may be a tradeoff in small-bodied leapers between the necessity for more rigid calcanei, versus the need for an overall lighter hindlimb, and as a result, lighter calcanei. Decreasing distal limb mass is especially important for small-bodied leapers given that a lighter animal is capable of leaping further, with greater velocity and acceleration than a heavier animal generating the same musculotendinous forces (Biewener, 2003; Emerson, 1985; Marsh, 1994). Thus, perhaps a more critical parameter for optimizing leap performance for a small-bodied leaper is distal limb mass (Peters & Preuschoft, 1984). Numerous studies have demonstrated distal limb mass reduction in relation to cursoriality and leaping (Hildebrand, 1985), accomplished via decreases in distal limb muscle mass (e.g., Payne, Hutchinson, Robilliard, Smith, & Wilson, 2005; Smith, Wilson, Jaspers, & Payne, 2006; Williams, Payne, & Wilson, 2007) and/or decreases in cortical bone mass via Haversian remodeling (Lieberman, Pearson, Polk, Demes, & Crompton, 2003; but see Skedros, Sybrowsky, Parry, & Bloebaum, 2003 for alternative explanations for decreasing distal bone mass). Decreasing bone volume in the distal segments of the limb may be advantageous for decreasing both distal limb mass and overall mass, thereby increasing leap performance. Calcaneus cortical bone volume fraction (i.e., cortical bone volume relative to total solid

bone volume), which is likely correlated to calcaneus mass, was not studied here but is worth investigating in the future to test this hypothesis.

Although the present study only analyzes the calcaneus, examining bone strength of the navicular would also be informative. In small-bodied leapers, both the calcaneus and the navicular are elongated, and Hall-Craggs hypothesized that these two tarsals perform different functional roles in the foot of prosimians (1966). Hall-Craggs' model (1966) suggests that in the ankle of galagids and tarsiers, the calcaneus acts as a rigid, propulsive lever for achieving powerful plantarflexion at the talocrural joint, while the navicular acts as a mobile, rotatory element for eversion and inversion of the intertarsal joints, which is especially important in primates due to their grasping feet. Gebo's (1987) subsequent detailed examination of foot and ankle anatomy of galagids and tarsiers via dissections and xeroradiographs revealed that while both taxa are capable of inversion and eversion at the intertarsal joints and mobility of the navicular in particular, the navicular in tarsiers has greater mobility than in galagids. Gebo found that tarsiers achieve more movement at the intertarsal joints facilitated by a highly mobile navicular (with a ball-and-socket-like configuration of the navicular-cuneiform joints), while galagids have less mobility at the navicular-cuneiform joints, but more movement at the calcaneal-cuboid joint (1987). This previous work suggests that the navicular plays a critical functional role in foot movements of leaping prosimians and its cross-sectional properties could inform future work on hindlimb adaptations to leaping.

In summary, while relative distal calcaneal elongation itself is an accurate indicator of leaping locomotion in small-bodied prosimians and can be used to infer leaping locomotion in fossil primates (e.g., Boyer et al., 2013), the data presented in the current study suggest that some aspects of internal cortical structure of the calcaneus may also be informative for understanding the mechanical principles underlying hindlimb leaping adaptations. Specifically, our data suggest that although small-bodied, specialized galagid leapers do not have relatively stronger calcanei than more quadrupedal galagids, they do exhibit calcaneal cross-sectional shapes indicative of predominantly single-plane loading. Whether small-bodied primate leapers may prioritize decreases in calcaneal bone volume over increases in calcaneal bone strength remains unknown. Future work on this question, as well as studying the cross-sectional properties of the elongated navicular, and sampling more small-bodied prosimians (i.e., tarsiers and cheirogaleids) will shed light on the biomechanics of calcaneal elongation in specialized leaping primates.

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DATA AVAILABILITY STATEMENT

The μ CT data that form the basis of this study are available by request in MorphoSource Project P530: "Primate Leaping and Bone Functional Adaptation" (www.morphosource.org). All raw data analyzed here are listed in Table S1.

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SUPPORTING INFORMATION

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