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Phenotypic Plasticity of Climbing-Related Traits in the Ankle Joint of Great Apes and Rainforest Hunter-Gatherers

VIVEK V. VENKATARAMAN,^{1*†} THOMAS S. KRAFT,^{1†} JEREMY M. DESILVA,²
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Abstract The “negrito” and African “pygmy” phenotypes are predominately exhibited by hunter-gatherers living in rainforest habitats. Foraging within such habitats is associated with a unique set of locomotor behaviors, most notably habitual vertical climbing during the pursuit of honey, fruit, and game. When performed frequently, this behavior is expected to correlate with developmentally plastic skeletal morphologies that respond to mechanical loading. Using six measurements in the distal tibia and talus that discriminate nonhuman primates by vertical climbing frequency, we tested the prediction that intraspecific variation in this behavior is reflected in the morphology of the ankle joint of habitually climbing human populations. First, to explore the plasticity of climbing-linked morphologies, we made comparisons between chimpanzees, gorillas, and orangutans from wild and captive settings. The analysis revealed significant differences in two climbing-linked traits (anterior expansion of the articular surface of the distal tibia and increased degree of talar wedging), indicating that these traits are sensitive to climbing behavior. However, our analyses did not reveal any signatures of climbing behavior in the ankles of habitually climbing hunter-gatherers. These results suggest that the detection of fine-grained differences in human locomotor behaviors at the ankle joint, particularly those associated with arboreality, may be obscured by the functional demands of terrestrial bipedalism. Accordingly, it may be difficult to use population-level characteristics of ankle morphology to make inferences about the climbing behavior of hominins in the fossil record, even when facultative arborealism is associated with key fitness benefits.

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Anthropologists of the early twentieth century debated whether the African “pygmy” and Asian “negrito” phenotypes were the result of recent shared ancestry or convergent evolution. Recently, this *pygmäenproblem* (Schmidt 1910) or pygmy question (Haddon 1912) has been the subject of renewed interest, fueled in part by mitochondrial DNA and Y-chromosome haplotype data. Recent studies suggest that African pygmies and Asian negritos are more closely related to other African and Asian populations, respectively, than they are to each other (Endicott et al. 2003, 2006; Thangaraj et al. 2003, 2005). A recent genome-wide study of single-nucleotide polymorphisms (SNPs) even points to multiple independent origins of the negrito phenotype within Asia (HUGO Pan-Asian SNP Consortium 2009). The causes of such convergent evolution remain an issue of debate, but the strong association between small stature and the occupation of rainforest habitats implicates the environment as a driving factor (Perry and Dominy 2009).

Research on skeletal morphology (see Bulbeck this issue; Stock this issue) has offered some corroborating nongenetic perspectives on this issue but also emphasizes the complexity associated with inferring population history on the basis of skeletal characters. Although cranial traits have proven useful for testing hypotheses about relatedness between populations (Bulbeck this issue), a functional-morphological approach based on postcranial traits may be useful for inferring actual behaviors performed by ancient hunting and gathering populations. Here we investigate whether this hunting and gathering mode of subsistence in tropical rainforests is associated with diagnostic skeletal correlates, specifically in the ankle joint. In general, rainforest hunter-gatherers adopt foraging strategies that reflect targeted consumption of foods that provide nutritional and energetic rewards within carbohydrate-impooverished rainforest environments. Acquiring these foods necessitates significant amounts of climbing behavior and arboreal foraging (Bailey 1991; Endicott and Endicott 2008; Kraft et al. in press), which poses a stark contrast to the uniform locomotor behavior of industrialized populations (Devine 1985).

Correspondences between behaviors performed by contemporary people and their anatomical correlates (e.g., bone cross-sectional properties) have provided valuable reference points for inferring mobility and activity patterns of ancient humans. For example, tennis and baseball players, in addition to cricketers, exhibit bilateral asymmetry in some indices of forelimb robusticity (Jones et al. 1977; Shaw and Stock 2009; Warden et al. 2009), and rowers have more robust humeri than nonrowers (Weiss 2003). Such associations have allowed researchers to infer habitual use of watercraft among populations who exploit aquatic resources (Stock and Pfeiffer 2001) or habitual digging with sticks by Late Stone Age foragers (Stock and Pfeiffer 2004). Accordingly, we hypothesize that the foraging behaviors of rainforest hunter-gatherers induce loading patterns that could generate diagnostic skeletal correlates.

The present study focused on rainforest hunting and gathering populations that climb trees frequently, as determined from the ethnographic literature. Although humans are clearly adapted for terrestrial bipedal locomotion, the documentation of human tree climbing complicates the classical perception of humans as committed

terrestrial bipeds who are incompetent in trees (Latimer 1991; Latimer and Lovejoy 1990) and instead points to a more diverse locomotor repertoire (Devine 1985; Watanabe 1971). Climbing populations include both Philippine and Malaysian negritos in addition to African pygmies. All engage in a wide variety of positional and locomotor behaviors during foraging. Of the scarce resources readily available to humans in tropical rainforests, honey, ripe fruit, and game are highly prized (Endicott and Endicott 2008; Ichikawa 1981; Lye 2004) but also the most difficult to acquire because of their location in the rainforest canopy. Consequently, acquiring these resources can require frequent vertical-climbing behavior (Venkataraman et al. 2013). For example, Bailey and Headland (1991) reported that Efe men spend approximately 8% of time away from camp either climbing or perched in trees. During the honey season in African rainforests, pygmy populations spend substantial amounts of time searching for and acquiring honey, which comprises a large portion of caloric input during this period (Bailey 1991; Ichikawa 1981). Bailey (1991) reported that the Efe climb to an average of 19.1 m to acquire honey, and sometimes as high as 51.8 m. Climbing is similarly prevalent among Southeast Asian foragers. Endicott (1979) notes that Batek (negrito) foragers sometimes climb tall (>50 m) trees daily in the pursuit of honey, and Agta foragers have also been reported to climb trees (Evans 1937; Griffin and Estioko-Griffin 1985), as have the Batak (Eder 1999) and Andaman Islanders (Dutta et al. 1985). By any measure, these climbing behaviors are dangerous (Hewlett et al. 1986; Perry and Dominy 2009), yet they are associated with the acquisition of vitally important food items. The frequency of climbing among rainforest foragers and its inherent danger suggest that natural selection should favor safety- and efficiency-enhancing behaviors and anatomies.

Identifying skeletal signals of climbing has long been a focus of study by anthropologists interested in the reconstruction of behavior in the primate fossil record. Such features manifest in several parts of the postcranial skeleton through genetic adaptation or plastic mechanisms [e.g., the infraspinous region of the scapula (Green et al. 2012), scapular morphology (Green and Alemseged 2012), or phalangeal curvature (Richmond 1998)]. Some researchers have also called attention to the ankle joint as an area sensitive to loads associated with vertical-climbing behavior (DeSilva 2009; Latimer et al. 1987), which is the second most frequent locomotor behavior of great apes (Doran 1996). DeSilva (2008, 2009) demonstrated that chimpanzees engage in significant amounts of ankle dorsiflexion and inversion during climbing, an action that reduces the distance between the climber's center of mass and the substrate (Cartmill 1974). Such ankle flexion is expected to economize muscular effort during climbing, making vertical ascent safer and more efficient. It is also correlated with several traits in the shaft and articular surface of the distal tibia (DeSilva 2008, 2009). Among these traits, chimpanzees and other apes exhibit mediolaterally (ML) expanded anterior articular surfaces. This attribute is thought to dissipate compressive loads at the anterior portion of the tibia as it rolls over the talus during extreme dorsiflexion. Humans do not bear this trait, nor do most other anthropoid primates

(e.g., old-world monkeys) whose style of climbing does not necessitate excessive flexion at the tibiotalar joint (DeSilva 2009).

Here we consider whether humans who climb habitually bear traits associated with vertical-climbing behavior. This investigation is premised on observational and quantitative studies of hunter-gatherers who climb trees in a manner that is kinematically similar to chimpanzees (Dempsey et al. 2012; Endicott and Endicott 2008; Evans 1937; Isler 2005; Venkataraman et al. 2013). During this style of climbing (Venkataraman et al. 2013: Figure 1), the climber places his or her foot against the tree and “walks” upward, advancing the hands and feet alternately (Endicott and Endicott 2008; Evans 1937). This style of climbing, termed *changwod* by the Jahai in Malaysia (Evans 1937), is accompanied by substantial ankle dorsiflexion (mean \pm SD, $40.7^\circ \pm 5.14^\circ$; Venkataraman et al. 2013) that is statistically indistinguishable, but only marginally so ($p = 0.06$; Venkataraman et al. 2013), from the mean observed value for maximal dorsiflexion by chimpanzees ($45.5 \pm 7.1^\circ$; DeSilva 2009). Some humans, including hunter-gatherers, also climb with highly inverted feet and hyperflexed knees (Figure 1) as the plantar surface of the foot is placed against the tree surface with the hips in hyperabduction (Dempsey et al. 2012), termed the “frog” position (Peters 2001) or *chinbodn* by the Jahai in Malaysia (Evans 1937). Because ankle dorsiflexion and inversion involve movement at homologous joints (ankle and subtalar) in humans and chimpanzees (Calhoun et al. 1994; Corazza et al. 2005; DeSilva 2008; Driscoll et al. 1994; Kura et al. 1998), we hypothesize that climbing and nonclimbing humans will evince anatomical differences in the ankle joint.

This study aims to test the sensitivity of the distal tibia to fine-grained differences in locomotor behaviors at intraspecific scales. Previously, species-level differences in characters of the distal tibia were found to broadly reflect diversity in positional repertoires across taxa (DeSilva 2008). The primate postcranial skeleton, including both shaft elements and articular surfaces, is determined by genetic influences in addition to those from the mechanical environment (Buck et al. 2010; Lieberman et al. 2001; Lovejoy et al. 1999; Pearson and Lieberman 2004; Ruff et al. 2006). Studies examining the features of lower limb morphology, including the distal tibia, indicate that this bone is sensitive to environmental effects, although this relationship is complex and the mechanistic basis for such a relationship remains poorly understood (Lieberman et al. 2001; Ruff 1988). Buck et al. (2010) found that distal limb segments respond more to habitual loading than do proximal limb segments, which appear to be largely controlled by climatic factors. This is perhaps attributable to the fact that mammal joint surface areas tend to be smaller in distal elements, causing relatively higher stresses (Lieberman et al. 2001). Importantly, osteogenic responses to loading are greater in juveniles than in adults (Lieberman et al. 2001; Pearson and Lieberman 2004). For humans, the frequency of climbing and its performance during early life among many hunter-gatherer populations would suggest that the habitual use of arboreal resources could be reflected in skeletal morphology.¹ Climbing among rainforest hunter-gatherers usually begins at a young age, often before the age of seven (Endicott and Endicott 2008; Lye 2004;



Figure 1. Photograph of a Batek (negrito) child climbing in the *chinbodn* or “frog” style (photograph by Lye Tuck-Po, reproduced with permission).

Kraft et al. in press). Overall, there is abundant theoretical and empirical evidence to predict that variation in climbing-related loading history, particularly within an ontogenetic context, will generate diagnostic skeletal correlates.

To further elucidate the ontogenetic basis, phenotypic plasticity, and intraspecific variability of climbing-related traits in the ankle, we compared zoo and wild great ape specimens (*Pan*, *Pongo*, *Gorilla*), with the expectation that wild apes, which are more arboreal than their zoo counterparts (Lukas et al. 2003; Remis 1998; Ross and Lukas 2006), would evince stronger correlates of climbing in response to habitual loading. We also performed a comparative analysis on the great apes, as well as between climbing (African pygmy and negrito) and nonclimbing humans to determine whether documented differences in naturalistic climbing frequency manifest as skeletal correlates.

Methods

Skeletal Measurements. We examined several skeletal traits found by DeSilva (2008) to correlate with vertical climbing frequencies in wild primates: (1)

size-standardized dimensions of the talar facet of the distal tibia, (2) metaphyseal shape, (3) relative medial malleolus thickness, (4) depth of tibial articular surface, (5) tibial angle, and (6) talar wedging. The justification for measuring these traits is briefly described for each trait later and follows DeSilva (2008). We hypothesized that, relative to nonclimbing humans, habitually climbing populations will exhibit higher values for traits linked to vertical climbing by DeSilva (2008, 2009).

In this study we made five measurements with digital calipers on the distal tibiae and made one measurement of tali. We performed preliminary analyses on our data set and found that samples from the left and right elements did not differ significantly for any of the measurements. Because many of the specimens we studied had tibiae that were damaged or missing, the values reported here refer variously to available samples from the left or right legs. We also examined size-related patterns in each of the six measurements to test whether our analyses could be confounded by the effect of allometric scaling. We found that regressions between body size and all of the six measurements were nonsignificant with extremely low coefficients of determination ($R^2 < 0.02$), indicating that body size is not a confounding factor in the analysis.

Size-Standardized Anterior Width of the Distal Tibia. Size-standardized anterior width (SSAW) quantifies the relative increase in the bone of the anterior portion of the articular surface. DeSilva (2008, 2009) hypothesized that this increase in bone will assist in dissipating compressive loads as the contact point between the tibia and the talus shifts anteriorly during dorsiflexion.

Six measurements were taken on the anterior aspect of the left tibial-articular surface. Our methods followed DeSilva (2009) closely to ensure direct comparability between studies. Repeated measurements were taken four days apart and were found to be within 5% of each other. The following measurements were taken: (a) maximal mediolateral (ML) length of the anterior aspect of the articular surface, (b) the maximal ML length of the posterior aspect of the articular surface, (c) the maximal ML length at the midpoint of the articular surface, (d) the maximal anteroposterior (AP) width of the most medial aspect of the articular surface, (e) the maximal AP width of the most lateral aspect of the articular surface, and (f) the maximal AP width at the midpoint of the articular surface. The geometric mean was calculated by raising the product of the six measurements to the 1/6 power. To calculate SSAW, ML length of the anterior aspect of the articular surface was divided by the geometric mean, following the size-adjustment protocol established by Darroch and Mosimann (1985).

Metaphyseal Shape. We hypothesized that more bone in the ML dimension, resulting in a rectangular shape, would facilitate more mobility of the talocrural joint than a square-shaped distal tibia. This geometry of the metaphysis may also reflect skeletal adaptations for dissipating more ML-directed loads during inverted-foot climbing. AP-expanded metaphyses may better dissipate AP-directed loads, such as those incurred in parasagittal plane motions (e.g., bipedal walking).

The ML width of the tibial metaphysis was determined by measuring the maximal ML dimension at the point where the medial malleolus begins to curve medially, immediately superior to the distal articular surface. The maximal AP dimension was defined as the maximal width perpendicular to the ML dimension. The relative expansion of the metaphysis in the ML dimension relative to the AP dimension, which is hypothesized to reflect the mobility of the talocrural joint and/or ML-directed loads during climbing (DeSilva 2008), was defined as the ratio of the length of these measurements multiplied by 100.

Relative Medial Malleolus Thickness. Inversion at the talocrural joint shifts the contact point of the distal tibia onto the medial malleolus (Calhoun et al. 1994; Kura et al. 1998); thus, an ML-expanded malleolus would serve to dissipate loading in this region during inversion.

The thickness of the medial malleolus was measured at the midpoint at its superior junction with the articular surface of the distal tibia. Relative malleolus thickness, predicted to be associated with loading during ankle inversion, was calculated by dividing the thickness of the medial malleolus (MM) by the square root of the product of the mediolateral (MLmp) and anteroposterior (APmp) midpoint lengths of the tibial articular surface $[(MM/(MLmp \times APmp)^{1/2}) \times 100]$.

Depth of Tibial Articular Surface. This measure is taken to be a proxy for the mobility of the talocrural joint, with the prediction that a flatter tibia (in the AP direction) would facilitate more dorsiflexion. More curved tibia (more depth) would prevent a great degree of dorsiflexion because the anterior aspect of the tibia contacts the talar neck during dorsiflexion.

Photographs of tibiae were taken in lateral view with a size standard in the same plane as the measurement to be taken. Photographs were imported into the public domain software ImageJ version 1.46 (<http://rsbweb.nih.gov/ij/>), and the line tool was used to measure the distance between the anterior and most posterior distally extending lips of bone. Perpendicular to this line, another line was drawn to the point of maximal depth of the tibial articular surface. The depth of the articular surface, taken to be a proxy for ankle-dorsiflexion capability, was determined as the ratio of the length of these two lines multiplied by 100.

Tibial Angle. The tibial angle, defined as the angle formed between the long axis of the tibia and the articular surface at the distal end of the bone, is expected to reflect inversion capability. Climbers should bear higher angles compared with nonclimbers, indicating oblique orientations of the tibia over the foot.

The tibial angle is defined as the angle formed between the long axis of the tibia and the ankle-joint surface. We used a carpenter's contour guide to assess the plane of the ankle-joint surface. Tibiae were pressed into the carpenter's contour guide with the contour pins oriented parallel to the long axis of the tibial shaft. The impression was then laid flat, photographed, and then imported into the program ImageJ. With the angle tool, the tibial angle was calculated as the angle formed

between the plane of the articular surface and the long axis of the tibia (as judged by the straight contour pins).

Talar Wedging. Talar wedging is defined as the ratio of the maximal width of the talar trochlea at its most anterior aspect to the maximal width of the talar trochlea at its most posterior aspect. DeSilva (2008) found that this ratio produces results similar to those of a more complex calculation that models the talus as a cone. Similar to expanded SSAW, we hypothesize that an increased degree of talar wedging helps to dissipate loads incurred during extreme dorsiflexion.

Predictions. For each trait, we make the following predictions for intraspecific comparisons. For SSAW, metaphyseal shape, medial malleolus thickness, tibial angle, and talar wedging, we expect climbers to evince higher values caused by the mechanical effects of this behavior. For the depth of the tibial articular surface, climbers are expected to evince lower values. Interspecific comparisons and the functional interpretations of these analyses are discussed by DeSilva (2008, 2009). As such, in this study we were concerned largely with intraspecific variation, particularly with respect to human rainforest foragers.

Specimens. All human pygmy specimens used in this study were from the University of Geneva, Switzerland, and the Musée de l'Homme, Paris. The seven specimens from the University of Geneva labeled "Ituri pygmées" are likely from populations of Mbuti or Efe. Six of these specimens are male. The specimens from the Musée de l'Homme included skeletons from the Philippines labeled "Négrito" and eight African pygmies of variable origin, seven of which were BaBinga from Central Africa and one of which was from Gabon. The sex information for many of these specimens was available in Marquer (1972) and/or provided by W. L. Jungers or H. Kurki. It is not possible to know the activity profiles of the individuals used in this study.

Data on the distal tibia from the Geneva sample of Ituri hunter-gatherers were incorporated into another publication (Venkataraman et al. 2013) and are also included here. The present study also includes data on agriculturalist humans collected from the ninth- through twelfth-century Paleoindian Libben collection housed at Kent State University (Lovejoy et al. 1977), the Hamann–Todd collection at the Cleveland Museum of Natural History (CMNH), and an unprovenanced sample of human tibiae from the Department of Anthropology, University of Michigan. Body weights are known for the CMNH humans ($n = 35$), allowed us to test whether any of these measures scaled allometrically. DeSilva (2008, 2009) found no detectable differences between the populations, and thus we report combined results for all variables. We also compared male and female human pygmy and negrito specimens because females in these populations tend to avoid climbing (Ichikawa 1981) and would be expected to evince no skeletal signals of climbing behavior. However, our analysis indicated no difference between males and females from these populations for any of the measured traits (Table 1), and

Table 1. Comparisons between Sexes for Traits in the Distal Tibiae of Climbing Humans (African Pygmies and Philippine Negritos).

	AFRICAN PYGMY				PHILIPPINE NEGrito			
	n		WELCH'S TWO SAMPLE t-TEST		n		WELCH'S TWO SAMPLE t-TEST	
	MALES	FEMALES	DF	t-VALUE	MALES	FEMALES	DF	t-VALUE
SSAW	11	4	5.30	-0.57	3	4	4.18	-0.85
Metaphysis dimensions	5	3	5.72	-1.83	3	4	2.34	-1.61
Medial malleolus thickness	11	4	6.81	0.14	3	4	4.74	0.34
Depth of tibial articular surface	4	2	3.04	-1.24	3	4	2.26	-1.30
Tibial angle	4	3	3.98	1.45	2	3	3.00	-1.15

thus we report combined results hereafter. Data from wild ape specimens presented here were previously reported in DeSilva (2008, 2009). New data from zoo specimens of *Pan*, *Gorilla*, and *Pongo* are also included here.

Statistical Analyses. To test for differences between groups, we performed Welch two-sample *t*-tests, with the significance level set at $\alpha = 0.05$; all tests were one-tailed, reflecting our *a priori* hypothesis that climbing individuals (or populations) will exhibit specific traits relative to nonclimbing individuals (or populations). When more than two groups were compared, one-way analysis of variance (ANOVA) was used to assess differences among groups. Post-hoc comparisons were made with Tukey's honestly significant difference tests to examine the relationships between the three human groups in this study (nonclimbing humans, African pygmies, and Philippine negritos). Assumptions of normality for all statistical tests were assessed using Q-Q plots. Homogeneity of variance was tested for ANOVAs with modified robust Brown-Forsythe Levene-type tests, in addition to Bartlett's tests. All analyses were performed in R, version 2.15.1 (R Development Core Team 2012).

Results

Comparisons between Zoo and Wild Specimens of Great Apes

SSAW of Distal Tibia. Figure 2 shows results for intraspecific comparisons between zoo and wild specimens. SSAW (Figure 2A) for *Pan troglodytes* was significantly expanded in wild specimens compared with those from zoos ($t = 3.71$, $df = 9.57$, $p = 0.002$). We observed the same trend in *Gorilla gorilla* ($t = 3.71$, $df = 9.57$, $p = 0.0001$). SSAW did not differ between wild and zoo specimens for *Pongo* ($t = 1.3$, $df = 17.80$, $p = 0.10$).

Metaphyseal Shape. Figure 2B shows results for intraspecific comparisons between zoo and wild

specimens for metaphyseal shape. *Pan troglodytes* individuals from the wild had relatively larger ML widths than zoo individuals, but the difference was marginally insignificant ($t = 1.72$, $df = 10.87$; $p = 0.06$). Wild specimens of *Gorilla gorilla gorilla* did not differ statistically from zoo specimens ($t = 0.27$; $df = 19.13$; $p = 0.39$), nor did wild and zoo *Pongo* specimens ($t = -0.14$; $df = 15.03$; $p = 0.56$).

Medial Malleolus Thickness. Figure 2C shows results for intraspecific comparisons between zoo and wild specimens for medial malleolus thickness. *Pan troglodytes* from the wild and the zoo did not differ statistically ($t = 0.54$; $df = 9.40$; $p = 0.30$). Wild and zoo gorillas did not differ in this trait ($t = 0.87$; $df = 16.04$; $p = 0.22$), nor did wild and zoo *Pongo* ($t = 1.33$; $df = 12.99$; $p = 0.10$).

Talar Wedging. Figure 2D shows results for talar wedging. Talar wedging for *Pan troglodytes* was significantly greater in wild specimens compared with those from the zoo ($t = 5.02$, $df = 15.78$, $p < 0.0001$). The same trend was observed in *Gorilla* ($t = 4.73$, $df = 22.73$, $p < 0.0001$) and *Pongo* ($t = 4.23$, $df = 11.02$, $p = 0.0007$).

Comparisons within *Homo* and Wild *Pan* and *Gorilla*

SSAW of Distal Tibia. A one-way ANOVA revealed significant differences between the three human groups ($p = 0.01$; Table 2). Post-hoc Tukey's honestly significant difference multiple comparisons revealed that nonclimbing humans evinced higher SSAW compared with African pygmies ($p = 0.033$) but not Philippine negritos ($p = 0.13$). African pygmies and negritos did not differ statistically in SSAW (Table 2). Lowland gorillas (*G. g. gorilla*) evinced significantly higher SSAW than did mountain gorillas (*G. g. beringei*; $p < 0.001$; Table 2). Common chimpanzees (*P. troglodytes*) and bonobos (*P. paniscus*) did not have statistically different SSAW ($p = 0.56$; Table 2).

Metaphyseal Shape. A one-way ANOVA revealed no differences between climbing and nonclimbing human groups in metaphyseal shape ($p = 0.18$; Table 2). Lowland gorillas (*G. g. gorilla*) evinced significantly more bone in the ML direction than did mountain gorillas (*G. g. beringei*) ($p = 0.001$; Table 2). Common chimpanzees (*P. troglodytes*) and bonobos (*P. paniscus*) did not have statistically different metaphyseal shapes ($p = 0.56$; Table 2).

Medial Malleolus Thickness. A one-way ANOVA revealed significant differences between climbing and nonclimbing human groups ($p < 0.001$; Table 2). Post-hoc Tukey's honestly significant difference multiple comparisons show that nonclimbing humans have significantly thicker medial malleoli in the ML dimension than do both African pygmies ($p < 0.001$) and Philippine negritos ($p < 0.001$). The t -tests do not reveal any statistical difference between *Pan* species ($p = 0.30$) but show a significant difference between lowland and mountain gorillas ($p < 0.001$).

Depth of Tibial Articular Surface. One-way ANOVA did not reveal any differences between climbing and nonclimbing human groups for this metric ($p = 0.288$;

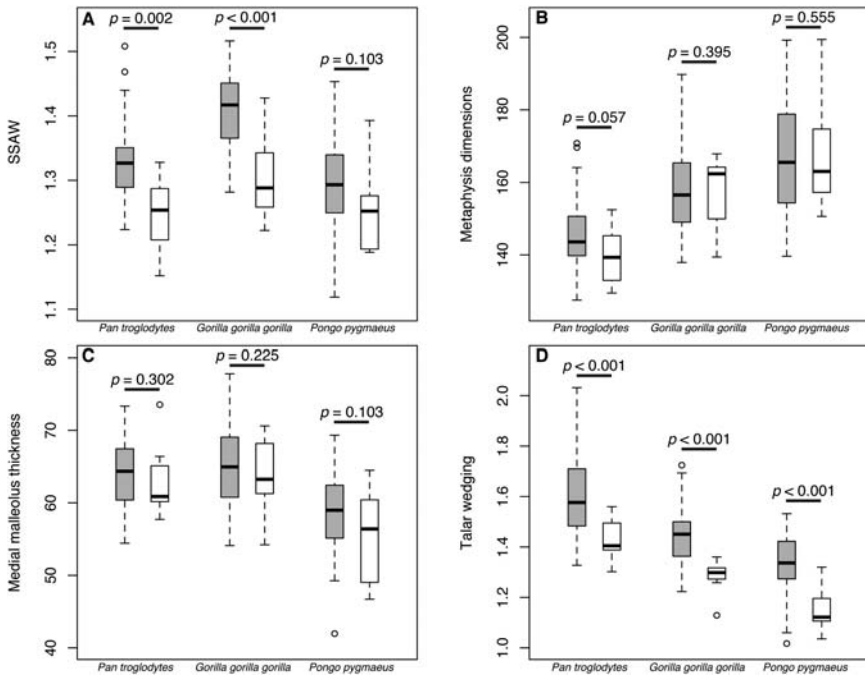


Figure 2. Intraspecific comparisons of the size-standardized anterior width of the distal tibia (SSAW; A), metaphysis dimensions (B), medial malleolus thickness (C), and talar wedging (D) for wild (gray) versus zoo (white) *Pan troglodytes*, *Gorilla gorilla gorilla*, and *Pongo pygmaeus*. Sample sizes for traits in the distal tibia (A–C) were as follows. *Pan troglodytes*: wild, $n = 49$; zoo, $n = 8$. *Gorilla gorilla gorilla*: wild, $n = 44$; zoo, $n = 11$. *Pongo pygmaeus*: wild, $n = 35$; zoo, $n = 10$. Sample sizes for talar wedging (D) were as follows. *Pan troglodytes*: wild, $n = 46$; zoo, $n = 8$. *Gorilla gorilla gorilla*: wild, $n = 44$; zoo, $n = 9$. *Pongo pygmaeus*: wild, $n = 33$; zoo, $n = 7$. Box plots show median (black bar), interquartile range (box), and ranges (whiskers), with outliers (values > 1.5 times the interquartile range) represented by circles.

Table 2), and lowland and mountain gorillas were statistically indistinguishable ($p = 0.91$).

Tibial Angle. A one-way ANOVA showed no differences between climbing and nonclimbing human groups ($p = 0.137$; Table 2).

Discussion

Previous work in skeletal biomechanics has suggested that diaphyseal and articular surface features of distal limb elements can respond plastically to habitual behaviors. Understanding the potential of the distal tibia to reflect habitual behaviors during life requires information about the developmental basis of traits in the

Table 2. ANOVA and Welch's *t*-Test Results for Comparisons within *Homo* and Wild *Pan* and *Gorilla*

	ANTERIOR WIDTH OF DISTAL TIBIA (SIZE STANDARDIZED)				METAPHYSIS DIMENSIONS				
	$\mu_i - \mu'_i$	df	<i>t</i>	<i>p</i>	$\mu_i - \mu'_i$	df	<i>t</i>	<i>p</i>	
<i>H. sapiens</i> × <i>H. sapiens</i> (African pygmy)	0.034	<i>a</i>		0.033	<i>b</i>			0.494	
<i>H. sapiens</i> × <i>H. sapiens</i> (negrito)	0.026			0.131				2.836	0.378
<i>H. sapiens</i> (African pygmy) × <i>H. sapiens</i> (negrito)	-0.008			0.9				5.916	0.166
<i>G. g. gorilla</i> × <i>G. g. beringei</i>	0.06	42.417	3.708	*** <0.001	10.650	32.231	3.290	** 0.001	
<i>P. troglodytes</i> × <i>P. paniscus</i>	-0.004	3.805	-0.164	0.561	6.348	3.257	0.968	0.2	

distal tibia. We compared zoo and wild specimens of vertically climbing great apes to test whether climbing-linked traits in the hominoid distal tibia result from phenotypically plastic osteogenic responses to habitual behaviors or genetically inherited growth patterns. This comparison is premised on the assumption that captive animals climb vertically less frequently than their wild counterparts. It should be stressed, however, that the individual locomotor profiles of the specimens used in this study are unknown.

Wild chimpanzees and gorillas displayed expanded SSAWs relative to captive conspecifics (Figure 2A). Wild chimpanzees also have ML-expanded metaphyses relative to zoo chimpanzees, but these differences do not extend to *Gorilla* or *Pongo*. The most parsimonious interpretation of the SSAW results is that vertical-climbing frequencies are higher among wild animals and that wild and zoo gorillas diverge in climbing frequencies to a greater extent than wild and zoo chimpanzees. This supposition is largely substantiated by comparisons of captive and wild great ape positional behavior (Doran and Hunt 1994; Lukas et al. 2003; Remis 1998; Ross and Lukas 2006), but it is difficult to conclusively demonstrate without further data on the locomotor habits of the individuals in the study. The lack of statistical significance in *Pongo* could be caused by a greater reliance on forelimb suspension and pedal grasping during locomotion; *Pongo* does not generally load the hind limb as much as other hominids do (Ruff 1988), often engages in "pulse climbing" (MacKinnon 1974), and climbs with the foot in a more elevated position relative to the hip joint than do African apes (Isler 2005). However, orangutans also engage in chimpanzee-like climbing (C. Knott, personal communication). It is also plausible that *Pongo* vertically climbs less frequently than does *Gorilla* or *Pan* (Remis 1998: table 5; but see discussion in Hunt 1991), yet the few data available for wild great apes are inconclusive: chimpanzees climb 96–117 m/day (Pontzer and Wrangham 2004), and orangutan females climb 55.7–121.4 m/day (Singleton et al. 2009).

MEDIAL MALLEOLUS THICKNESS				DEPTH OF TIBIAL ARTICULAR SURFACE				TIBIAL ANGLE (DEGREES)			
$\mu_i - \mu'_i$	df	<i>t</i>	<i>p</i>	$\mu_i - \mu'_i$	df	<i>t</i>	<i>p</i>	$\mu_i - \mu'_i$	df	<i>t</i>	<i>p</i>
11.907	c		*** <0.001	-0.39	d		0.765	-0.958	e		0.553
14.390			*** <0.001	0.66			0.407	-2.04			0.13
2.483			0.249	1.05			0.286	-1.083			0.626
6.362	30.585	3.594	*** <0.001	-0.90	42.818	-1.371	0.911				
1.602	3.374	0.582	0.299								

^aANOVA: $F = 4.662$; $df = 2, 172$; $p = 0.011$.

^bANOVA: $F = 1.744$; $df = 2, 98$; $p = 0.180$.

^cANOVA: $F = 120.1$; $df = 2, 171$; $p < 0.001$.

^dANOVA: $F = 1.262$; $df = 2, 95$; $p = 0.288$.

^eANOVA: $F = 2.068$; $df = 2, 50$; $p = 0.137$.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

A final possibility is that our analysis is underpowered, because we did detect statistically significant differences between wild and captive *Pongo* in the degree of talar wedging (Figure 2D).

Intersex differences in positional behavior among wild great apes and humans offer further potential for testing the sensitivity of traits in the distal tibia to climbing frequencies. Vertical-climbing frequency (as measured by percentage of time spent climbing) does not differ between male and female chimpanzees (Doran and Hunt 1994) or between male and female lowland gorillas (Remis 1998). Male mountain gorillas climb less than do female mountain gorillas (Remis 1998). As in some of the great apes, climbing frequency among humans differs between the sexes. Ethnographic studies of hunter-gatherers show that women tend to avoid climbing, although there are exceptions (Bailey 1991; Endicott and Endicott 2008; Lye 2004; Marlowe 2010). Our study of small-bodied humans found no evidence that traits in the distal tibia reflect these behavioral differences between males and females (Table 1).

In summary, we interpret skeletal metrics of the distal tibia to reflect genuine differences in vertical-climbing frequencies among wild populations and zoo populations. This finding has two key implications for evaluating intraspecific differences in locomotor behaviors. First, they suggest that these traits, particularly SSAW in the hominids, are phenotypically plastic in response to habitual loading and thus reflect ankle dorsiflexion and/or inversion during vertical ascent. Although it is possible that genetic constraints on the articular surface differ between *Pongo* and the African great apes, there is little evidence to support or refute such a possibility.

The comparative analysis of wild lowland and mountain gorilla populations is consistent with the finding that mountain gorillas prefer terrestrial substrates and climb less frequently than do lowland gorillas (Remis 1998). Lowland gorillas have higher SSAW, ML-expanded metaphyses, and ML-expanded malleoli than do mountain gorillas (Figure 3, Table 2). This result is also consistent with the finding that medial cuneiform morphology tracks hallucal-abduction ability and relative frequency of arboreality in *Gorilla* (Tocheri et al. 2011). Male mountain gorillas are less terrestrial than female mountain gorillas (Remis 1998), although our data do not reflect this for SSAW ($p = 0.48$), metaphysis dimensions ($p = 0.88$), or medial malleolus thickness ($p = 0.75$).

A second implication of the zoo-wild comparative analyses is that they afford an estimate of the *extent* of phenotypic plasticity associated with broadly known locomotor differences. Our comparisons between wild and zoo apes can be used to predict the extent to which locomotor differences can drive phenotypic plasticity in the distal tibia. Comparing zoo and wild values of SSAW for *Pan*, *Gorilla*, and *Pongo* produces differences of 6.5%, 7.6%, and 2.5%, respectively. It is important to note that SSAW is a composite measure of six variables; thus, changes in this variable cannot be easily attributed to a single cause. Nevertheless, these results illustrate that an expanded SSAW in climbing humans might be quite modest relative to that of nonclimbing humans. As such, even subtle sources of variability might obscure any signal of vertical climbing in the human distal tibia.

We detected no skeletal evidence of vertical climbing in the distal tibiae of individuals drawn from two rainforest hunter-gatherer populations that are known to climb frequently (Figure 3, Table 2). Numerous possibilities could account for this finding. First, the activity patterns of the studied individuals were unknown, despite their being drawn from habitually climbing populations, as judged from a combination of quantitative and anecdotal data in the ethnographic literature. An alternative possibility is that the loading regime associated with climbing by the individuals in this study was either inconsistent in direction or form, or performed infrequently. Direct comparison between vertical-climbing frequencies in humans and chimpanzees is complicated by the absence of quantitative data on human-climbing behavior. It is important to note that chimpanzees climb rather quickly (~ 0.5 m/s; see discussion in Pontzer and Wrangham 2004), whereas human tree climbing tends to be slow and deliberate, and performed relatively less often (Kraft et al. in press). This difference in climbing velocity and frequency could result in comparatively lower stresses in the ankles of climbing humans. The use of material culture by humans could be a further confounding factor if climbing can be simplified to avoid extreme flexions. Yet even assisted climbing can be accompanied by extreme flexions (Venkataraman et al. 2013). Many climbing populations, however, do frequently use unassisted climbing, and it is sometimes the preferred style of ascent (Kraft et al. in press). A final point is that our data represent population-level characteristics. Because of the social underpinnings of some climbing behaviors (e.g., some men excel at climbing and tend to specialize in honey acquisition; Ichikawa 1981), the absence of climbing signals at the

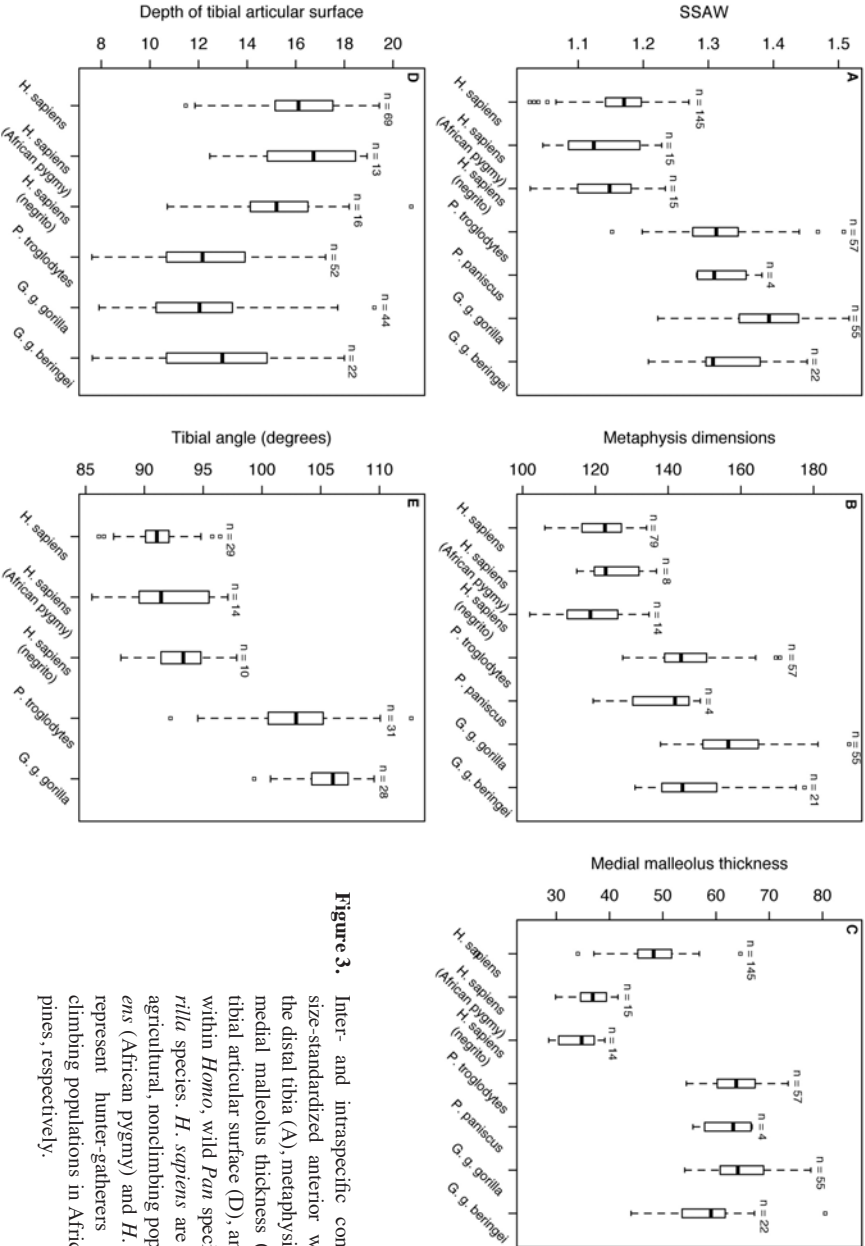


Figure 3. Inter- and intraspecific comparisons of the size-standardized anterior width (SSAW) of the distal tibia (A), metaphysis dimensions (B), medial malleolus thickness (C), and tibial angle (E) within *Homo*, wild *Pan* species, and wild *Gorilla* species. *H. sapiens* are individuals from agricultural, nonclimbing populations. *H. sapiens* (African pygmy) and *H. sapiens* (negrito) represent hunter-gatherers from habitually climbing populations in Africa and the Philippines, respectively.

population level is perhaps not surprising. Indeed, the small sample of specimens in our study with known sexes did not differ in distal-tibia morphology related to climbing behavior. Further research on the kinematics of human climbing that incorporate in vivo techniques will be necessary to gauge the impact of climbing behavior on skeletal growth in humans.

In fact, and contrary to our predictions, SSAW and medial malleolus thickness differed between climbing and nonclimbing humans (Figure 3). Individuals from climbing populations had significantly less anteriorly expanded distal tibiae and thinner medial malleoli, suggesting that other behaviors in the locomotor repertoire, such as walking, may exert an opposing influence to that of climbing (Table 2). Furthermore, uneven terrestrial substrates common to rainforest habitats might require an increased stabilization of the ankle joint during walking. As such, any efforts to identify skeletal correlates of behaviors performed by rainforest hunter-gatherers, particularly climbing, must consider the full diversity of the human locomotor repertoire and the trade-offs therein, in addition to population-specific ecologies.

Nevertheless, the discordance between a population-level behavior and skeletal morphology raises questions about our ability to detect fine-grained signatures of habitual locomotion in an arboreal milieu. Honey acquisition is all but invisible in the archaeological record (Laden 1992), yet it is a key component of foraging strategies among modern and ancient hunter-gatherer populations, and potentially for earlier hominins (Wrangham 2011). For instance, the Efe and Mbuti eat enormous quantities of honey for several months during the year, a habit that requires frequent climbing and clambering. Our study examined a suite of traits in the ankle, but other anatomies of the foot, knee, hip, back, and shoulder may also contribute to the extraordinary climbing abilities of hunter-gatherers. For example, the ontogeny of scapular morphology was used recently to infer substantial amounts of climbing behavior in *Australopithecus afarensis* (Green and Alemseged 2012). Our study suggests that the detection of fine-grained differences in human locomotor behaviors at the ankle joint, particularly those involving arboreality, may be obscured by the demands of terrestrial bipedalism. It may thus be difficult to use population-level characteristics of ankle morphology to make inferences about the climbing behavior of hominins in the fossil record, even when facultative arborealism is associated with key fitness benefits.

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Note

1. Lovejoy et al. (1999) provide a useful framework for interpreting the influences of genetics and habitual behaviors on observed skeletal morphologies. They note that morphologies can either *reflect* or *permit* functions, depending on their developmental origins. As discussed in the text, the traits in question likely reflect both genetic influences and behavior during life and should therefore be considered to reflect and/or permit the studied movements.

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