

Locomotor behavior and long bone morphology in individual free-ranging chimpanzees

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Abstract

We combine structural limb data and behavioral data for free-ranging chimpanzees from Tai (Ivory Coast) and Mahale National Parks (Tanzania) to begin to consider the relationship between individual variation in locomotor activity and morphology. Femoral and humeral cross sections of ten individuals were acquired via computed tomography. Locomotor profiles of seven individuals were constructed from 3387 instantaneous time-point observations (87.4 hours). Within the limited number of suitable chimpanzees, individual variation in locomotor profiles displayed neither clear nor consistent trends with diaphyseal cross-sectional shapes. The percentages of specific locomotor modes did not relate well to diaphyseal shapes since neither infrequent nor frequent locomotor modes varied consistently with shapes. The percentage of arboreal locomotion, rather than estimated body mass, apparently had comparatively greater biological relevance to variation in diaphyseal shape. The mechanical consequences of locomotor modes on femoral and humeral diaphyseal shapes (e.g., orientation of bending strains) may overlap between naturalistic modes more than currently is recognized. Alternatively, diaphyseal shape may be unresponsive to mechanical demands of these specific locomotor modes. More data are needed in order to discern between these possibilities. Increasing the sample to include additional free-ranging chimpanzees, or primates in general, as well as devoting more attention to the mechanics of a greater variety of naturalistic locomotor modes would be fruitful to understanding the behavioral basis of diaphyseal shapes.

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Introduction

Structure of the postcranial skeleton reflects aspects of an animal's locomotion (Alexander, 2003). The link between behavior and body plan has been established through a combination of investigative approaches. The current understanding of an osseous response to mechanical stimuli (Martin et al.,

1998; Currey, 2002) is based on a wealth of studies conducted over the last 40 years (e.g., Heřt et al., 1969, 1971, 1972; Lišková and Heřt, 1971; Lanyon and Rubin, 1984; Rubin and Lanyon, 1984; Gross et al., 1997; Judex et al., 1997). Experimental studies in controlled settings (e.g., Rubin and Lanyon, 1982; Biewener et al., 1983; Biewener and Taylor, 1986; Davies et al., 1993; Blob and Biewener, 1999, 2001; Lieberman et al., 2003, 2004) have quantified the mechanics of locomotor modes, particularly strain regimes experienced by limb long bones; however, relatively few have emphasized primates (Lanyon et al., 1975; Fleagle et al., 1981; Swartz

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et al., 1989; Burr et al., 1996; Demes et al., 1998, 2001). It is clear that dynamic behaviors (locomotor modes) rather than static behaviors (postural modes) drive osseous responses.

Some transcend methodological limitations in laboratory and naturalistic conditions by incorporating free-ranging specimens into analyses of long bone structural properties (e.g., Schaffler et al., 1985; Burr et al., 1989; Ruff and Runestad, 1992; Demes and Jungers, 1993; Terranova, 1995a,b; Jungers et al., 1998; Ruff, 2002; Carlson, 2005). Although substantial intragroup morphological variation has been a unifying theme, even when subspecific comparisons are investigated (Carlson, 2005), group-wide behavioral assessments have been used in functional interpretations. If idiosyncratic behavioral distinctions are visible as individual variation in diaphyseal cross-sectional properties, then functional signals in cross-sectional properties may be undervalued when generalizing behavioral repertoires across groups. Although infrequently used at an individual level, long-term observational studies of free-ranging primates provide quantitative locomotor behavior data (e.g., Fleagle, 1977; Fleagle and Mittermeier, 1980; Hunt, 1991, 1992; Doran, 1993, 1996; Garber and Pruett, 1995; Remis, 1998). Our aim is to consider individual variation in morphology and locomotor behavior in order to compare bone structure and locomotion in free-ranging individuals. This represents the first such comparison of which we are aware.

Cross-sectional geometric properties provide a non-destructive, non-invasive means of estimating the ability of a bone to resist deformation by assuming that long bone diaphyses can be modeled as beam structures (Martin et al., 1998). It generally is presumed that bone distribution is influenced by activity patterns of the individual (Meyer, 1867; Roux, 1881; Wolff, 1892; Pauwels, 1968; see recent review in Pearson and Lieberman, 2004). However, using cross-sectional properties to decipher loading history of long bones is complex (Bertram and Swartz, 1991). For instance, bone modeling rates decline over the duration of skeletal growth (Martin et al., 1998), and at different rates depending upon the skeletal element of interest (Lieberman et al., 2003). Thus, an osseous response to mechanical stimuli also depends partly upon age and skeletal location. Others (e.g., Lovejoy et al., 2003) have suggested that diaphyseal shape does not reflect life history or activity patterns, but rather it is a reflection of developmental history (e.g., shared genetic relationships).

Superstrate or substrate reaction forces (SRFs) that arise during locomotion frequently generate dynamic bending loads in limb long bones when coupled with the gravitational force acting on body mass (i.e., body weight). Body weight support, however, also creates an axial component within load regimes. Torsion, or twisting about a longitudinal diaphyseal axis, is yet a third component. The extent to which SRF and body weight vectors are aligned in three-dimensions is important in determining the loading regime experienced by long bones. Bending is known to dominate most forms of mammalian locomotion, but bones are also likely to fail under torsion (Rubin and Lanyon, 1982; Biewener and Taylor, 1986; Demes et al., 2001; Lieberman et al., 2004). When bending and axial compressive loads [or tensile loads (Swartz et al., 1989)] are superimposed, a neutral axis of bending will not pass through

the centroid of a cross section (Demes et al., 1998, 2001; Lieberman et al., 2004).

The ratio of the principal moments of area (PMAs) compares maximum and minimum resistance to bending deformation, and is considered a reliable indicator of *how* a limb is used during locomotion (Schaffler et al., 1985). Even when an experimentally-derived neutral axis of bending neither passes through the centroid nor aligns particularly well with the principal axis of a cross section, as *in vivo* studies indicate (e.g., Lieberman et al., 2004), the ratio of PMAs (I_{max}/I_{min}) calculated about principal axes passing through the centroid will still reflect circularity of a diaphyseal cross section (i.e., shape). With a PMA ratio close to one, a cross section will resemble a cylinder.¹ Cross sections with values diverging from one become increasingly elliptical. When shape properties are considered, a cylinder should be equally resistant to bending deformations from a variety of orientations, whereas an ellipse should be unequally resistant to bending deformations from the same variety of orientations. Thus, it follows that a more circular diaphysis should be capable of resisting bending deformations from a wider variety of orientations than a more elliptical diaphysis.

Arboreal locomotion may incorporate more diversity in the orientation of diaphyseal bending regimes than terrestrial locomotion (Schaffler et al., 1985; Burr et al., 1989; Runestad et al., 1992; Demes and Jungers, 1993; Carlson, 2005). Experimental studies of several primate limb bones (e.g., humeri, ulnae, tibiae) support greater variability in bending load orientations during arboreal behaviors such as brachiation (Swartz et al., 1989) and climbing (Demes et al., 2001) relative to variability observed during linear terrestrial quadrupedalism (e.g., Demes et al., 1998, 2001). Studies of external forces experienced during locomotion also support greater multi-directional force orientation during arboreal locomotion relative to terrestrial locomotion. Substrate reaction forces (SRFs) experienced by two lemur species (*Eulemur fulvus* and *Lemur catta*) more regularly alternated between a medially-directed and laterally-directed force during a given limb contact when a simulated arboreal support was used as opposed to a terrestrial support (Carlson et al., 2005). Greater variation in the mediolateral (ML) reaction force direction associated with arboreal quadrupedalism was attributed to balancing the center of mass over the narrow simulated branch. Finally, observational studies of primates in their natural habitats indicate that limbs are abducted during arboreal locomotion to a greater extent, and more variably overall, than during terrestrial locomotion (see definitions in Hunt et al., 1996).

While cross-sectional geometric properties may reflect behavioral patterns in part, they also are strongly correlated with body mass (Jungers et al., 1998; Ruff, 2003). Even shape ratios, such as ML vs. anteroposterior (AP) bending rigidity, correlate strongly with body mass ($r = 0.940$; Ruff and Runestad, 1992). Body mass, has a critical influence on primate

¹ A square also has a PMA ratio of 1, but it is less realistic to assume a square shape than a cylindrical shape for a diaphyseal cross section from a long bone.

locomotor repertoires (Napier, 1967; Cartmill and Milton, 1977; Fleagle and Mittermeier, 1980; Crompton, 1984; Fleagle, 1985), and must be controlled for when comparing cross-sectional properties of individuals. In a previous study, PMA ratio, relative to ML/AP ratio, exhibited generally weaker correlations with body mass in a sample of roughly 20 African apes with associated body masses (Carlson, 2005). If a shape ratio (e.g., PMA ratio) is to be a particularly meaningful measure of *how* a limb is used, it would be useful to determine how well it reflects locomotor behavior as opposed to body size.

Here we present unique data in order to explore individual variation in femoral and humeral diaphyseal shapes, locomotor repertoires, and estimated body masses. We emphasize previously introduced relationships between arboreal/terrestrial locomotor behavior and diaphyseal shape, between typical irregular/regular gait patterns and diaphyseal shape, and between arboreal locomotion and diaphyseal shape versus body size and diaphyseal shape.

Materials and methods

Pan troglodytes schweinfurthii at Mahale Mountains (Tanzania) and *P. t. verus* at Taï Forest (Côte d'Ivoire) National Parks have been studied for approximately 35 and 25 years, respectively (Nishida, 1990; Boesch and Boesch-Achermann, 2000). Cross-sectional data were acquired from femoral and humeral diaphyses of ten adult individuals whose remains were collected upon their death (Table 1). Mahale individuals

are stored in the Laboratory of Human Evolution, Kyoto University, Japan. Taï individuals are stored in the Anthropologisches Institut der Universität Zürich, Switzerland.

Only adults were included in the sample. Bone modeling rates drop dramatically upon skeletal maturity; adults are less responsive to load regime changes than growing individuals (Ruff et al., 1994; Martin et al., 1998; Lieberman et al., 2003). Since chimpanzees are known to exhibit ontogenetic changes within locomotor repertoires (Doran, 1992, 1997), this raises the possibility that adult morphological variation (e.g., PMA ratios) may be less tuned to adult locomotor behavior variation and more reflective of non-adult locomotor behavior variation. However, chimpanzees attain adult-like locomotor profiles around age 6 (Doran, 1992, 1997), which substantially precedes the cessation of their primary growth around age 12 (females: Leigh and Shea, 1995) to 14 (males: Goodall, 1986). This extent of growth following adoption of an adult-like locomotor profile strongly suggests that ample time exists to affect diaphyseal modeling.

Recovery of complete skeletons is seldom possible in free-ranging groups, thus bilateral femora and humeri were not available for all individuals, and sample sizes varied between comparisons. Seven of the ten individuals had associated behavioral data collected over the course of long-term observational studies. These seven individuals provide the basis for shape ratio and behavioral comparisons, while all ten individuals were used to compare shape ratios and estimated body masses. The interval between behavioral observations and death varied,

Table 1
Sample information

Individual	Locality	Sex	Estimated age (yrs)*	Estimated body mass (kg) [†]	Behavioral data	Elements	Femoral length [‡] (mm)	Humeral length [§] (mm)
Agathe	Taï	F	15	31.6	no	both femora and humeri	274 (269)	293 (292)
Bijou	Taï	F	19	41.4	yes	right femur, both humeri	NA (260)	296 (292)
Kiri	Taï	F	23	32.1	yes	both femora and humeri	262 (265)	282 (278)
Ondine	Taï	F	38	34.2	yes	both femora and humeri	271 (272)	303 (301)
Fitz	Taï	M	19	42.6	yes	left femur	282 (NA)	NA (NA)
Kendo	Taï	M	25	51.2	yes	right femur, left humerus	NA (283)	307 (NA)
Betty	Mahale	F	23	30.1	no	both femora, left humerus	263 (264)	253 (NA)
Pulin	Mahale	F	20	27.8	yes	both femora and humeri	266 (264)	263 (265)
Wansombo	Mahale	F	>40	36.0	no	both femora and humeri	264 (264)	269 (270)
Musa	Mahale	M	36	35.9	yes	both femora and humeri	242 (241)	242 (243)

F = female, M = male. NA = not available. Values from right elements are in parentheses.

* Taï values reported by Boesch and Boesch-Achermann (2000); Mahale values reported by Hosaka et al. (2000).

† Body mass estimates derived from right and left femora averages when possible. Body mass estimated using a reduced major axis (RMA) regression equation derived from 25 African apes of known body mass (Carlson, 2002). With this equation, 80% of the individuals had predicted body masses within 20% of their reported body masses: $10^{bm} = 3.030(10^{fmsid}) + (-2.946)$, where bm = body mass (kg) and $fmsid$ = femoral head superior-inferior diameter (mm).

‡ Femoral lengths reported as mechanical lengths for Taï specimens (see definition in Carlson, 2005) and physiological length for Mahale specimens (see definition in Gunji et al., 1998).

§ Humeral lengths reported as maximum length for Taï specimens (see definition in Carlson, 2005) and total length for Mahale specimens (see definition in Gunji et al., 1998).

thus we must assume that observed locomotor repertoires were broadly representative of peri-mortem repertoires. In order to maximize behavioral samples, we did not control for potential complicating factors such as seasonality and rank.

Digital images of diaphyseal cross sections were acquired via computed tomography (CT). Elements were studied at three sites per diaphysis (35%, 50%, and 65% lengths). Region of interest (ROI) at 35% and 65% length correspond to mid-distal and mid-proximal diaphyses, respectively. Left and right femora or humeri were treated separately. This created 12 ROIs: three each for left femora (F left), right femora (F right), left humeri (H left), and right humeri (H right).

Image data acquisition

Tai specimens were scanned using a conventional CT scanner (Picker PQ 5000, Picker International) located in the Department of Radiology, Kantonspital, Winterthur, Switzerland. Scan parameters and protocol were similar to those published elsewhere (see Ruff, 2002; Carlson, 2002, 2005). Ipsilateral femora and humeri from the same individual were scanned simultaneously in order to use scanning time most efficiently, as well as to facilitate future analyses and data storage.

Mahale specimens were scanned using a spiral CT scanner (TSX-002/4I, Toshiba Medical Systems Co., Ltd.) located in the Department of Zoology, Kyoto University. Scan parameters have been published elsewhere (see Yamanaka et al., 2005). Single long bones were centered in the scanner's field of view (FOV), and positioned such that serial images of cross sections perpendicular to the longitudinal diaphyseal axis were obtained. The FOV corresponds to the metric dimensions of an image, and when combined with image matrix size (usually 512×512), will provide information about pixel size (e.g., mm/pixel). Since serial scans rather than single slice scans were used for Mahale specimens, ROIs of 35%, 50%, and 65% lengths were identified by isolating images that contained proximal and distal reference

points (see definitions in Carlson, 2005) and then counting the number of intervening images (e.g., 200 images). Since slice thickness and increment were constant during data acquisition, images were spaced evenly along diaphyses. Thus, images could be identified in a straightforward fashion (e.g., 35% ROI is 200 images \times 0.35 = image 70, etc.).

Morphological data collection

Digital images of Mahale and Tai long bones were analyzed with Scion Image (release Beta 4.0.2; ported from NIH Image for Macintosh by Scion Corporation and freely available at <http://www.scioncorp.com>). A full-width half-maximum (FWHM) threshold for determining bone/air boundaries was altered to create a mean FWHM threshold (Ohman, 1993; Carlson, 2005). This tailored bone/air thresholds to individual cross sections, thus minimizing threshold error due to taphonomic and/or biological variation in material properties between or within cross sections. Scion Image macros modeled after the SLICE program (Nagurka and Hayes, 1980) were used to calculate standard cross-sectional properties.

Cross-sectional area of a beam is proportional to its ability to resist deformation under axial compression. Gravitational force acting on body mass, and resisted by the supporting limbs, is responsible for axial compression in diaphyses. Thus, it is appropriate to standardize total area (TA) and cortical area (CA) to body mass. Bending loads experienced by a beam are proportional to the product of the applied force (e.g., body weight) and beam length. Hence, the product of estimated body mass and length (see Table 1 for definitions) was chosen to standardize bending rigidity measurements (I_x , I_y , I_{max} , I_{min}). Scaled properties were reported to facilitate future comparisons with other datasets. Scaling factors are eliminated when ratios are constructed (i.e., $[I_{max}] [\text{scaling factor}]^{-1} / [I_{min}] [\text{scaling factor}]^{-1} = I_{max}/I_{min}$). Means and standard deviations for unstandardized and standardized cross-sectional properties are

Table 2
Unstandardized cross-sectional properties

	F35% <i>n</i> = 8 (9)	F50% <i>n</i> = 8 (9)	F65% <i>n</i> = 8 (9)	H35% <i>n</i> = 9 (7)	H50% <i>n</i> = 9 (7)	H65% <i>n</i> = 9 (7)
TA (mm ²)	367.26 (372.85) 51.07 (50.10)	364.73 (372.96) 50.34 (49.68)	360.27 (367.83) 42.72 (48.25)	311.64 (299.26) 53.89 (38.63)	325.44 (317.97) 54.96 (39.91)	337.82 (325.77) 61.69 (40.81)
CA (mm ²)	234.59 (227.34) 36.74 (24.31)	256.14 (249.76) 42.39 (31.68)	258.02 (253.01) 43.37 (34.56)	202.03 (187.60) 32.42 (22.60)	205.65 (193.21) 33.57 (21.72)	202.52 (189.05) 36.17 (22.75)
I_x (mm ⁴)	8073.4 (7904.6) 2011.8 (1641.3)	8420.6 (8377.9) 2052.2 (2039.7)	8189.0 (8370.3) 1963.7 (2417.3)	6712.1 (6137.0) 2231.8 (1611.7)	8292.1 (7686.4) 2945.1 (1855.4)	8212.4 (7435.1) 2825.3 (1513.9)
I_y (mm ⁴)	11004.6 (11253.1) 3395.9 (3116.8)	11255.2 (11754.8) 3544.0 (3157.1)	11031.1 (11443.4) 2539.7 (2692.9)	7042.5 (6201.9) 2014.3 (954.8)	6666.5 (6092.1) 2070.0 (1128.5)	7491.7 (6581.9) 3149.3 (1222.7)
I_{max} (mm ⁴)	11195.1 (11324.9) 3478.8 (3108.0)	11498.0 (11868.5) 3578.3 (3113.6)	11215.9 (11688.3) 2593.4 (2939.4)	7385.7 (6548.6) 2058.3 (1249.9)	8457.8 (7796.8) 2984.3 (1900.9)	8568.7 (7688.9) 3076.7 (1679.5)
I_{min} (mm ⁴)	7882.9 (7832.8) 1868.2 (1649.3)	8177.8 (8264.1) 1955.5 (2058.6)	8004.2 (8125.4) 1910.0 (2124.5)	6368.8 (5790.4) 2124.2 (1298.7)	6500.8 (5981.7) 2026.8 (1058.0)	7135.4 (6328.2) 2930.6 (1150.8)
I_{max}/I_{min}	1.40 (1.43) 0.13 (0.16)	1.39 (1.43) 0.11 (0.14)	1.41 (1.45) 0.14 (0.14)	1.18 (1.14) 0.08 (0.06)	1.29 (1.29) 0.11 (0.14)	1.22 (1.22) 0.15 (0.17)

F = femur, H = humerus; 35% = mid-distal diaphysis, 50% = midshaft diaphysis, 65% = mid-proximal diaphysis. Values from right elements are in parentheses. Mean in first row of cells, one standard deviation in second row. Second moments of area, I_x and I_y , correspond to bending rigidity about x- and y-axes, respectively.

Table 3
Standardized cross-sectional properties*

	F35% <i>n</i> = 8 (9)	F50% <i>n</i> = 8 (9)	F65% <i>n</i> = 8 (9)	H35% <i>n</i> = 9 (7)	H50% <i>n</i> = 9 (7)	H65% <i>n</i> = 9 (7)
sTA (mm ² /kg)	10.90 (10.60) 1.06 (0.98)	10.84 (10.62) 1.18 (1.14)	10.72 (10.47) 1.02 (1.08)	8.85 (8.82) 1.26 (1.15)	9.23 (9.38) 1.19 (1.27)	9.56 (9.61) 1.13 (1.28)
sCA (mm ² /kg)	6.99 (6.53) 1.00 (1.06)	7.63 (7.17) 1.12 (1.19)	7.69 (7.26) 1.17 (1.26)	5.74 (5.55) 0.60 (0.81)	5.86 (5.74) 0.85 (0.96)	5.78 (5.62) 0.98 (1.01)
sI _x (mm ³ /kg)	0.89 (0.84) 0.14 (0.08)	0.93 (0.89) 0.14 (0.09)	0.91 (0.88) 0.11 (0.10)	0.66 (0.64) 0.10 (0.12)	0.82 (0.81) 0.14 (0.16)	0.82 (0.79) 0.14 (0.15)
sI _y (mm ³ /kg)	1.21 (1.19) 0.23 (0.15)	1.24 (1.24) 0.25 (0.19)	1.22 (1.22) 0.18 (0.16)	0.70 (0.66) 0.09 (0.07)	0.66 (0.65) 0.09 (0.11)	0.73 (0.70) 0.13 (0.12)
sI _{max} (mm ³ /kg)	1.23 (1.19) 0.25 (0.16)	1.27 (1.26) 0.26 (0.19)	1.25 (1.24) 0.18 (0.16)	0.74 (0.69) 0.09 (0.08)	0.84 (0.82) 0.15 (0.17)	0.85 (0.82) 0.16 (0.17)
sI _{min} (mm ³ /kg)	0.87 (0.83) 0.11 (0.07)	0.91 (0.87) 0.12 (0.09)	0.89 (0.86) 0.12 (0.10)	0.63 (0.61) 0.09 (0.09)	0.65 (0.64) 0.09 (0.10)	0.70 (0.67) 0.11 (0.10)

F = femur, H = humerus; 35% = mid-distal diaphysis, 50% = midshaft diaphysis, 65% = mid-proximal diaphysis. Values from right elements are in parentheses. Mean in first row of cells, one standard deviation in second row.

* Total area (TA) and Cortical area (CA) are standardized by dividing estimated body mass into raw values. Other cross-sectional properties (i.e., I_x, I_y, I_{max}, and I_{min}) are standardized by dividing the product of estimated body mass and bone length into raw values. Standardized second moments of area, sI_x and sI_y, correspond to bending rigidity about x- and y-axes, respectively.

reported in Tables 2 and 3, respectively. However, given the sample sizes, comparative statistics are not attempted.

Due to varying times of discovery, it was impossible to directly measure body mass in the field; instead, femoral head supero-inferior (SI) diameter was used as a proxy. Using this measure, Ruff (2003) reported a 77% success rate for body mass prediction errors of ≤20% in a sample of 22 primates, including one African ape. Carlson (2002) estimated body masses for 25 African apes of known mass and found that about 80% had predicted values within 20% of actual mass. We used Eq. (1), based on Carlson (2002), for estimating body mass. When possible, body mass estimates were averaged from left and right femora of an individual.

$$\log_{10}(\text{bm}) = 3.030(\log_{10}\text{fmsid}) + (-2.946) \quad (1)$$

where bm = body mass (kg), fmsid = Femoral head SI diameter (mm)

Behavioral data

Behavioral percentages (Table 4) were derived from the classification of Carlson (2005), and behavioral definitions follow Hunt et al. (1996) as strictly as possible (but see Carlson, 2002, 2005). In order to maximize behavioral samples, substrate categories were combined for comparisons of specific locomotor modes. For example, arboreal and terrestrial quadrupedal walking categories were combined into a “total quadrupedal walking” category. Most quadrupedal walking, however, was observed on terrestrial substrates. Other specific behavioral modes (i.e., quadrupedal climb, quadrupedal scramble, and suspensory) were observed almost exclusively in arboreal settings.

Table 4
Behavioral data

	Time Points (<i>n</i>)	Total locomotor (%)*	Total quad walk (%)	Total quad climb (%)	Total quad scramble (%)	Total suspend (%)	Arboreal locomotor (%)	Terrestrial locomotor (%)
Bijou	365	18.08	90.91	3.03	1.52	0	15.15	84.85
Kiri	406	9.11	91.89	5.41	0	2.70	13.51	86.49
Ondine	575	21.22	95.08	4.10	0	0.82	5.74	94.26
Fitz	66	13.64	100.00	0	0	0	11.11	88.89
Kendo	117	12.82	86.67	13.33	0	0	13.33	86.67
Pulin	1267	19.02	92.53	4.98	0.41	1.66	9.96	90.04
Musa	591	16.75	92.93	3.03	1.01	2.02	13.13	86.87
<i>P. t. verus</i> [†]	F	15.75	85.63	9.29	1.89	1.45	18.20	81.80
	M	15.97	86.61	8.33	1.37	1.09	14.70	85.30
<i>P. t. schweinfurthii</i> [†]	F	13.59	91.49	5.96	1.23	0.95	12.02	87.98
	M	14.57	93.85	4.27	0.26	0.60	8.20	91.80

F = female, M = male.

* Total locomotor % corresponds to the number of observations involving any form of locomotion as a percentage of all recorded focal observations of an individual.

† Comparable subspecies percentages for Tai (*P. t. verus*) and Mahale (*P. t. schweinfurthii*) chimpanzees reported in Carlson (2005).

Data analysis

Scatter plots are provided for comparisons of interest. Spearman’s rank correlations were used for comparing associations between shape and arboreal locomotion percentage (ALP), and between shape and estimated body mass. While correlation *p*-values are reported, they are not assessed for significance since comparative strength of associations was of greater interest than absolute strengths of either association. Correlation analyses were performed in SPSS 11.0.1 (SPSS Inc., Chicago, IL).

Results and discussion

Shape and arboreal locomotion

Scatter plots of ALP and PMA ratios are depicted for each ROI of femoral and humeral diaphyses (Fig. 1a-f). Left and right PMA ratios are combined in plots. Clear trends are absent, although the scatter of 35% and 65% femoral PMA ratios is generally from the lower left to the upper right. In 35% and 65% humeral ROIs (Fig. 1d,f), PMA ratios tend to decrease as ALP increases. In a majority of individuals for

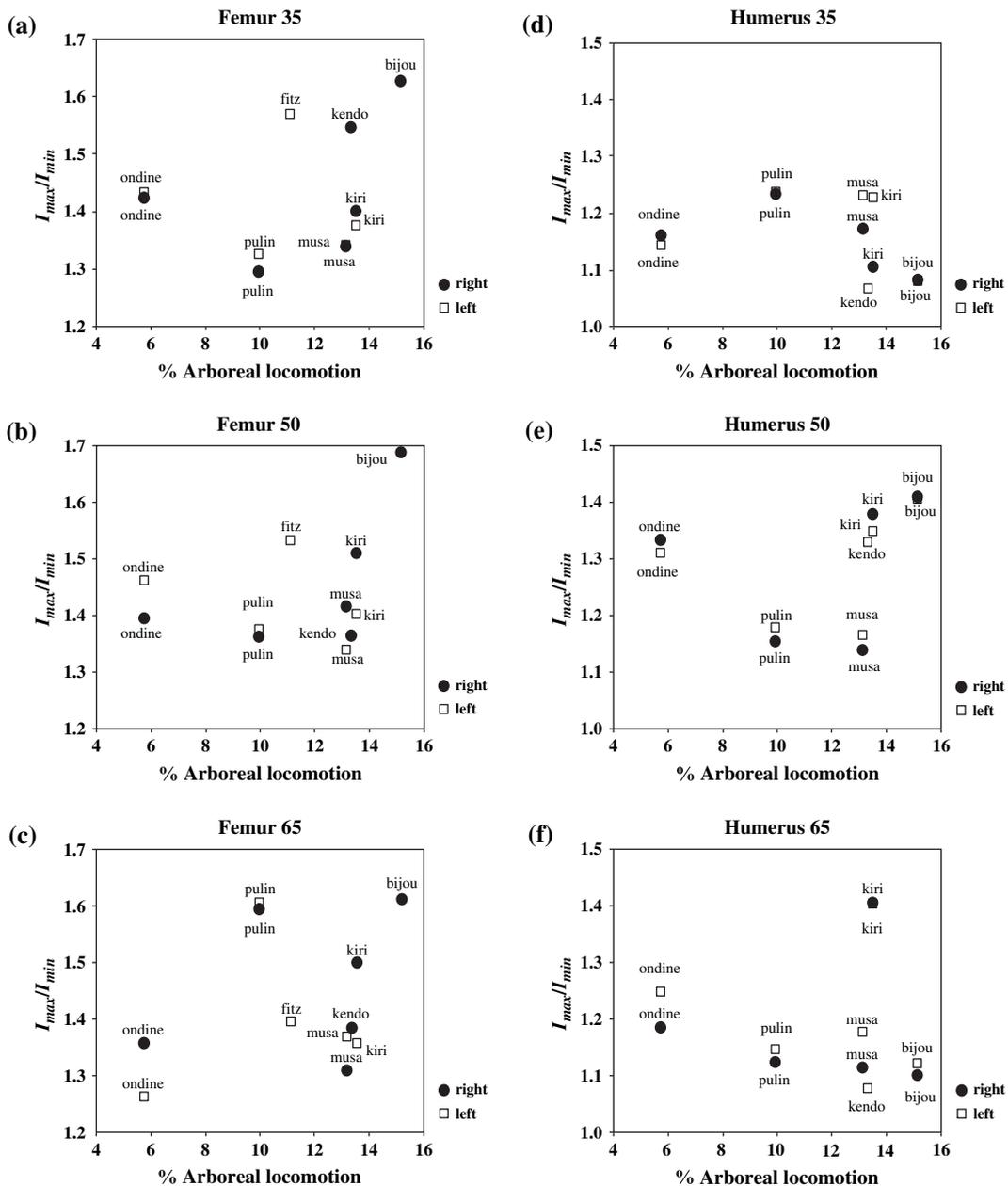


Fig. 1. Principal moment of area ratios (I_{max}/I_{min}) characterizing shape are plotted against percentages of arboreal locomotion for those individuals with associated behavioral data. Plots for each ROI are reported separately (but sides are combined): femur 35% diaphyseal length (a), 50% length (b), 65% length (c), and humeral 35% diaphyseal length (d), 50% length (e), and 65% length (f). Right elements are represented by filled circles, while left elements are represented by open squares.

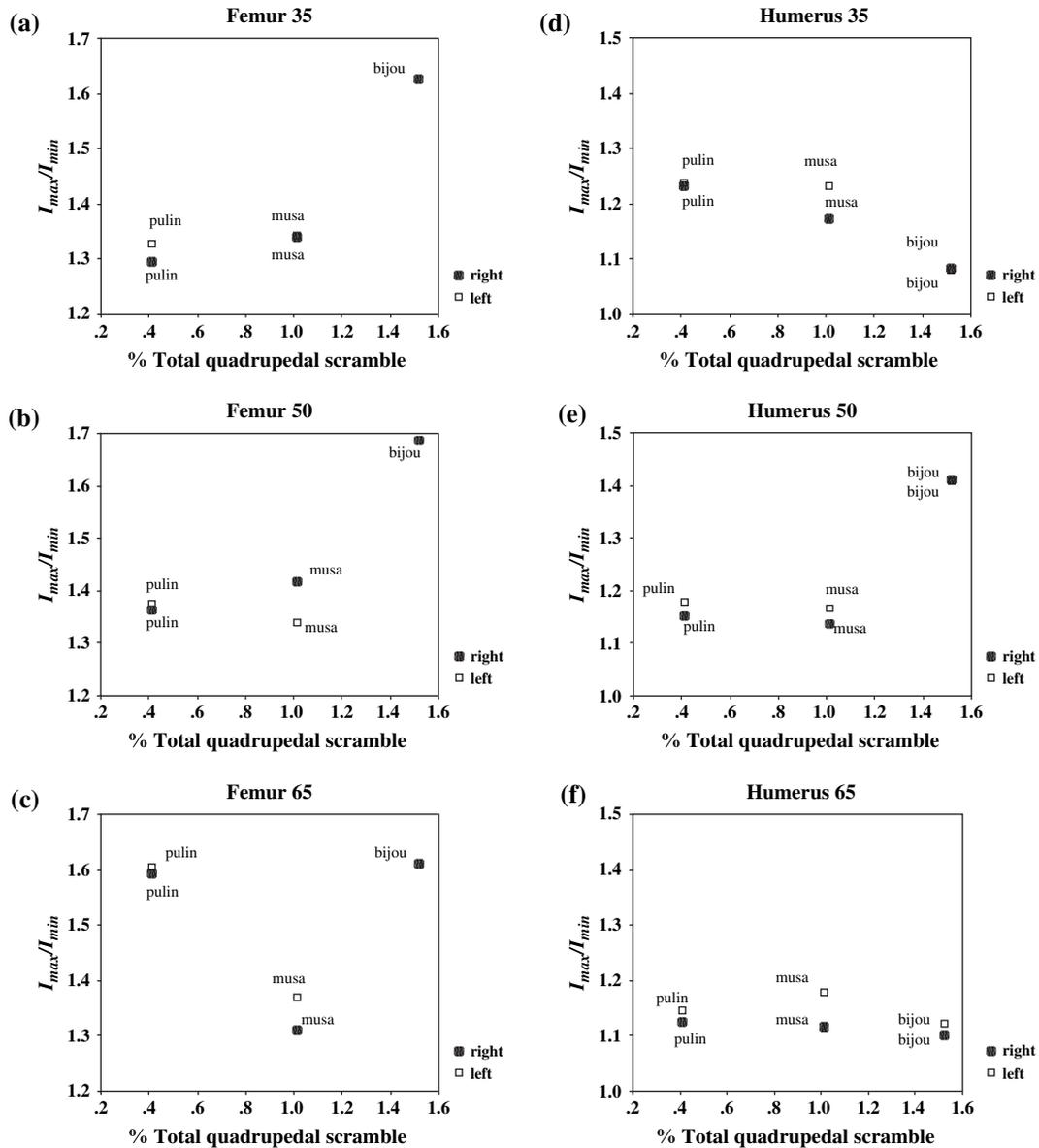


Fig. 2. Principal moment of area ratios (I_{max}/I_{min}) characterizing shape are plotted against percentages of total quadrupedal scrambling for those individuals with non-zero percentages. All scrambling was observed in arboreal substrates. Plots for each ROI are reported separately (but sides are combined), as in the legend of Fig. 1a–f. Right elements are represented by filled circles, while left elements are represented by open squares.

which bilateral data are available, within-individual differences in PMA ratios (i.e., bilateral asymmetry) usually are less than between-individual differences (i.e., compare between-individual and within-individual separation along the y-axis). Kiri, and to a lesser extent Ondine and Musa, often exhibit the greatest bilateral asymmetry in PMA ratios. The Mahale chimpanzees (Musa and Pulin) usually group together amongst Taï chimpanzees in the y-axis of plots (PMA ratios) despite their behavioral differences. Ondine, the Taï female who has a noticeably lower ALP than other individuals, exhibits no consistent relationship in PMA ratio relative to other individuals.

The lack of apparent trends in Fig. 1, particularly when comparing Ondine to other individuals, underscores the complexity of interpreting cross-sectional properties when

discussing behaviorally-induced variability apart from genetically-induced variability. Among free-ranging primates, arboreal locomotion generally encompasses a greater array of locomotor behaviors (e.g., scrambling, suspensory, climbing, quadrupedal walking) than terrestrial locomotion (e.g., quadrupedal walking, running) (Hunt et al., 1996). Increased behavioral diversity associated with the use of discontinuous arboreal substrates is presumed to introduce more variability into the loading regimes experienced by limb bone diaphyses. Among individuals with large behavioral samples, locomotor repertoires were similarly broad even though arboreal locomotor behavior percentages varied by up to 10% of total locomotion. Focusing on individuals who exhibited more behaviorally diverse repertoires, a consistent relationship between PMA ratios and ALP also was not observed.

Shape and scrambling

Scatter plots of PMA ratios and percentages of total quadrupedal scrambling are reported for individual femoral and humeral ROIs (Fig. 2a-f). Left and right PMA ratios are combined in plots. There are no consistent trends across all ROIs. For 35% and 50% ROIs (Fig. 2a-b, d-e), Mahale chimpanzees (Musa and Pulin) are more similar in PMA ratios than either is to the Tai chimpanzee (Bijou), despite Bijou and Musa having more similar behavioral percentages.

While scrambling exhibits the lowest percentage of observed locomotor behavior in Table 4, a locomotor mode need not be frequent in a repertoire to stimulate bone formation. Umemura et al. (1997) demonstrated elevated bone

formation (i.e., cortical area) in exercised rats that performed as few as five jumps per day, or as many as 100. It is reasonable to suspect that scrambling in the African ape locomotor repertoire would not be more rare by comparison, particularly compared to rats performing only five jumps per day. It remains unknown, however, whether scrambling behavior in primates is as high impact a behavior as jumping in rats.

Shape and quadrupedal walk

Scatter plots of PMA ratios and percentages of total quadrupedal walk are organized by ROI, with left and right ROIs combined in plots (Fig. 3a-f). Excluding Kendo, who had the fewest behavioral time point data, only weak trends

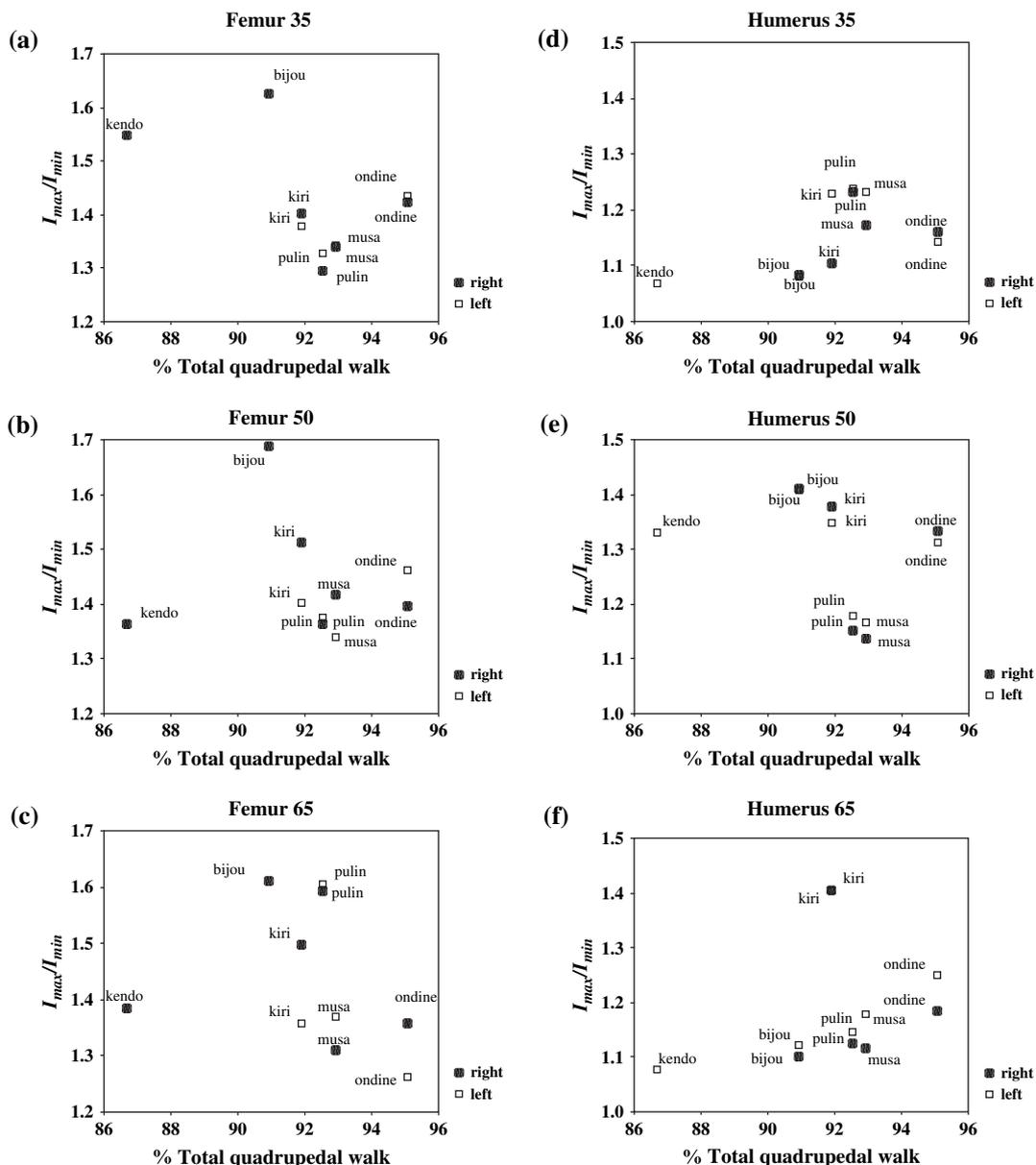


Fig. 3. Principal moment of area ratios (I_{max}/I_{min}) characterizing shape are plotted against percentages of total quadrupedal walking for those individuals with associated behavioral data (excluding Fitz). A majority of quadrupedal walking was observed in terrestrial substrates. Plots for each ROI are reported separately (but sides are combined), as in the legend of Fig. 1a-f. Right elements are represented by filled circles, while left elements are represented by open squares.

are visible. Femoral points are scattered from the upper middle to lower right regions of plots. Mahale chimpanzees (Musa and Pulin) often cluster together amongst Tai chimpanzees, except at the 65% femoral ROI (Fig. 3c).

Specific locomotor modes of low (e.g., scrambling) or high (e.g., quadrupedal walk) percentage exhibited equally poor trends with PMA ratios. A similar result was reported in a comprehensive examination of African apes, by species and subspecies (Carlson, 2005). The lack of differentiation between the relationship of shape ratio and presumably low frequency erratic behaviors versus the relationship between shape ratio and presumably high frequency stereotypical behaviors underscores the need for caution when using diaphyseal shapes to infer specific behavioral components in locomotor repertoires of extinct taxa (e.g., MacLatchy et al., 2000; Madar et al., 2002).

Behavior versus body size

Shape ratios generally exhibit higher correlations with ALP than with estimated body mass (see Table 5). In other words, variation in ALP rather than estimated body mass seems to associate more tightly to variation in shape ratios.

General conclusions

Maneuverability can be highly desirable in many free-ranging terrestrial and arboreal animals (Dickinson et al., 2000). The terrestrial landscape is littered with obstacles around which animals must navigate, whereas the arboreal landscape is a mixture of discontinuously positioned substrates and superstrates. Scrambling behavior arguably represents the ultimate embodiment of maneuverability in arboreal substrates (see definitions in Hunt et al., 1996). Experiments suggest that arboreal locomotion is characterized by more multi-directional external forces (e.g., ML forces change direction during stance phase more

frequently) than is terrestrial quadrupedal locomotion in lemurs, potentially as a result of balance requirements (Carlson et al., 2005). In addition, direction changes result in higher ML peak forces (McClay et al., 1994; Demes et al., submitted for publication) than have been observed during linear locomotion in either arboreal or terrestrial settings (Ishida et al., 1990; Schmitt, 2003; Carlson et al., 2005). Thus, arboreal locomotor modes may generate strains of relatively high magnitude and variable orientation, particularly when they are defined by irregular gait patterns. The functional consequences of turning also may be an integral feature of locomotion in general, not only arboreal locomotion.

The fact that Ondine, the most behaviorally distinguished individual in terms of ALP, did not stand out among shape ratios provides a cautionary note when inferring locomotor repertoires from diaphyseal shape. Her apparently idiosyncratic behavioral differences were not similarly distinguishable among PMA ratios.

Clearly, however, the small sample restricts applicability of these data. More data are needed before the existence of trends in the scatter plots can be decided. Locomotor diversity may have been under-sampled since some individuals exhibited zero frequencies for several specific locomotor behaviors (e.g., see Fitz). However, although particular locomotor modes may have been performed rarely by these individuals, it is unlikely that they were avoided completely. Nonetheless, when considering behavioral data more broadly, individuals often exhibited percentages of arboreal locomotion that corresponded to subspecies estimates (Table 4). On this basis, broader behavioral comparisons such as the percentage of arboreal versus terrestrial locomotion appear representative.

Further work is necessary to clarify the nature of behavioral signals in diaphyseal shape. A more sophisticated measure than PMA ratio may offer a more precise means of identifying trends in shape variability. Behavioral studies quantifying pervasiveness of direction changes within locomotor repertoires

Table 5
Spearman's correlation results comparing shape associations with arboreal locomotion percentage (% arb locomotion) and estimated body mass

ROI	n^\dagger	Shape vs. % arb locomotion	Shape vs. body mass*	ROI	n^\dagger	Shape vs. % arb locomotion	Shape vs. body mass*
F35 (left)	5,8	-0.100 (0.873)	0.167 (0.693)	H35 (left)	6,9	-0.429 (0.397)	-0.667 (0.050)
F35 (right)	6,9	0.543 (0.266)	0.300 (0.433)	H35 (right)	5,7	-0.700 (0.188)	-0.107 (0.819)
F50 (left)	5,8	-0.300 (0.624)	0.143 (0.736)	H50 (left)	6,9	0.771 (0.072)	-0.050 (0.898)
F50 (right)	6,9	0.714 (0.111)	0.017 (0.966)	H50 (right)	5,7	0.600 (0.285)	<0.001
F65 (left)	5,8	<0.001	-0.167 (0.693)	H65 (left)	6,9	-0.257 (0.623)	-0.650 (0.058)
F65 (right)	6,9	0.543 (0.266)	-0.050 (0.898)	H65 (right)	5,7	-0.400 (0.505)	-0.750 (0.052)

Region of interests (ROIs): F = femoral, H = humeral. 1st row of cells reports Spearman's correlation coefficients, 2nd row of cells reports associated p -values in parentheses.

† Sample sizes for shape vs. % behavior to the left of the comma, sample sizes for shape vs. body mass to the right of the comma.

* Femoral head SI diameter used as a proxy measure. When bilaterally available, the average was used in correlation analyses.

of free-ranging animals also would be informative. The consensus on positional mode classifications, however, does not provide a means (e.g., a mode) with which to address this aspect of the behavioral continuum. Finally, expanding the sample of both morphological and associated locomotor behavior data from free-ranging primates, while particularly challenging, is of the utmost importance.

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