Long bone structural proportions and locomotor behavior in Cercopithecidae

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ABSTRACT

Limb bone articular and diaphyseal proportions have been shown to relate to locomotor behavior in broad comparisons across catarrhines, but comparisons among phylogenetically and functionally more closely related species may be particularly useful in investigating form-function relationships that can be applied to fossil taxa. Here we compare inter- and intra-limb proportions of diaphyseal strength and articular surface area and breadth of the femur and humerus with frequencies of leaping and vertical climbing behavior in 13 cercopithecid species. Leaping frequency is highly positively correlated with femoral/humeral diaphyseal strength, moderately positively correlated with femoral/humeral articular breadth, and less highly correlated with femoral/humeral articular surface area. These results are consistent with predicted higher bending loads as well as joint reaction forces on the femora of leapers. Surface areas may show a weaker association because they also directly impact joint excursion and are thus more influenced by other aspects of locomotion, including climbing. Climbing frequency is positively correlated with humeral head articular surface area/diaphyseal strength, but weakly negatively correlated with femoral head articular surface area/diaphyseal strength. These combined trends lead to a strong negative association between climbing and femoral/humeral head surface area. Femoral/humeral diaphyseal strength and distal articular breadth are not correlated with climbing frequency. The climbing results are consistent with greater shoulder mobility in more frequent vertical climbers. The lack of such a relationship in the femur among these taxa contrasts with earlier findings for catarrhines more generally, including hominoids, and may be a result of different climbing kinematics in cercopithecoids involving less hip abduction than in hominoids. Different use of the forelimb during climbing in cercopithecoids and hominoids may also explain the lack of association between femoral/humeral diaphyseal strength and climbing in the present study, in contrast to comparisons across catarrhines more generally.

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1. Introduction

Accurate reconstruction of locomotor behavior in the fossil record is dependent upon detailed assessments of behavioral-morphological relationships among extant taxa (Day, 1979). This is true even when fossil taxa exhibit morphologies not observed among living species, including mosaic combinations or intermediate expression of traits (MacLatchy et al., 2000; Ruff, 2002).

Examination of closely related extant taxa may be particularly valuable in such situations, by highlighting the extent to which relatively subtle behavioral gradients are reflected in morphological variation (Fleagle, 1976b; Rodman, 1979; Fleagle and Meldrum, 1988; Gebo and Sargis, 1994; Dunham et al., 2017; Ruff et al., 2018a).

Inter- and intra-limb proportions of long bone diaphyseal strength and articular size have been shown to be related to locomotor behavior in both broad (Schultz, 1953; Schaffler et al., 1985; Demes and Jungers, 1993; Terranova, 1995; Connour et al., 2000; Ruff, 2002) and narrow (Burr et al., 1989; Demes and Jungers, 1989; Demes et al., 1991; Gebo and Sargis, 1994; Runestad, 1997;

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Ruff et al., 2013, 2018a) taxonomic groupings of primates. To date, however, similar studies of cercopithecoids have been relatively limited, focusing primarily on diaphyseal scaling and general shape characteristics, with structural properties derived from photon absortiometry (Burr et al., 1989; Jungers and Burr, 1994; Jungers et al., 1998), or have involved analyses of single specimens (Gebo and Sargis, 1994).

In the present study, limb bone structural proportions of 13 species within the family Cercopithecidae are determined using computed tomography and compared with frequencies of leaping and climbing behavior in these taxa. These locomotor categories were chosen for analysis because of their significance in behavioral classifications and the ecology of both extant and extinct primate taxa (Fleagle, 1976a; Fleagle et al., 1981; Andrews and Aiello, 1984; Gebo, 1989; McCrossin et al., 1998; Ryan et al., 2012; Hunt, 2016). We also incorporate phylogenetic comparative methods in these analyses, following demonstration of significant phylogenetic signal in bone structural parameters (O'Neill and Dobson, 2008).

The specific morphological traits examined here are torsional/average bending strength of the femoral and humeral diaphyses, femoral and humeral head articular surface areas, and femoral and humeral proximal and distal articular breadths. All of these traits are potentially functionally relevant in that they should be related to mechanical loading of the bones as well as joint excursion (Ruff, 1988, 2002; Godfrey et al., 1991; Rafferty and Ruff, 1994; Polk et al., 2000; Hammond, 2014). A previous study of catarrhines demonstrated that increased frequency of locomotor behaviors involving slower, more cautious movements and/or a variety of limb positioning, e.g., vertical climbing, clambering, and suspension, is associated with larger joints (particularly articular surface areas) relative to diaphyseal strength; increased frequency of forelimb suspension and climbing is associated with greater forelimb to hind limb diaphyseal strength; and increased frequency of leaping is associated with greater hind limb to forelimb strength (Ruff, 2002). Here we examine these relationships in a taxonomically narrower and morphologically more homogeneous group of Old World monkeys. Specifically, we test the following predictions: 1) femoral to humeral diaphyseal strength will be positively correlated with frequency of leaping; 2) for both the femur and humerus, articular surface area of the head relative to diaphyseal strength will be greater in more frequent climbers; 3) femoral to humeral proximal and distal articular breadths will be greater in more frequent leapers; 4) femoral to humeral head articular surface areas will be greater in more frequent leapers, but the correlations will be lower than for breadths, since surface areas should be influenced by both joint loading and joint excursion (Godfrey et al., 1991; Rafferty and Ruff, 1994; Ruff, 2002).

2. Materials and methods

2.1. Samples and locomotor behavior

Femora and humeri from a total of 162 individuals and 13 species were included in the study (Table 1; Fig. 1). For some species, indicated in Table 1, sample sizes were somewhat reduced depending upon availability of particular elements; sample sizes included in each analysis are indicated in Results. Bone structural data for six species (*Papio hamadryas cynocephalus*, *Macaca nemestrina*, *Macaca fascicularis*, *Colobus guereza*, *Trachypithecus cristatus*, and *Presbytis rubicunda*) were derived from a previous study of museum specimens (Ruff, 2002). Data for the remaining seven species were obtained for this study from naturally deceased animals collected in the Taï National Park, Ivory Coast (Dunham et al., 2015, 2017). All individuals were adults, with fully fused long bone epiphyses, except for one *Cercocebus atys* specimen, in which the

distal femoral and proximal humeral epiphyses were only partially fused. Bone lengths and articular breadths for this individual (a male) were close to mean values for other adult male *Cer. atys*, so it appears to have been very near skeletal maturity. To maximize sample sizes in some of the taxa represented by only a few individuals (Table 1), and because in behavioral studies locomotor data were often either pooled or reported for only one sex, or the two sexes did not differ greatly in locomotor profiles within species, males and females were pooled for all analyses.

Locomotor data were obtained from field studies of wild populations, with the main sources of information listed in Table 1. Frequencies of climbing and leaping as percentages of total locomotor behavior, combined over both traveling and foraging, were recorded or calculated from the data given in each study (see below for details). Secondary sources were also consulted when available. All data (except as noted) were for adult, fully habituated animals.

Behavioral data for the Taï species were reported by McGraw (1998:Table 1, 2000:Table 2). Definitions of 'leaping' and 'climbing' generally followed Fleagle (1977), i.e.: leaping = "Progression between discontinuous supports using primarily rapid extension of the hindlimb for propulsion [...] landing involves use of both hind limbs and forelimbs"; climbing = "vertical ascent in which the arms reach above the head and pull the animal up while the hindlimbs alternatively push the body up" (McGraw, 1998:495). Fleagle (1977:298, 1978:247) actually used a somewhat broader definition of climbing: "continuous progression, often vertical, using various combinations of three or more limbs. Arms are used primarily to pull the body up while hindlimbs push." This incorporates potential lateral movements and diverse limb positioning commonly referred to as 'clambering' in other studies (Cant, 1988; Gebo and Chapman, 1995). Difficulties in precisely defining 'climbing' have often been noted in the literature (Rose, 1979; Fleagle et al., 1981; Gebo and Chapman, 1995; Hunt et al., 1996; Moffett, 2000). Following Hunt et al. (1996), here we include only vertical movements at angles to the horizontal of 45° or more as climbing, although as discussed below, it was not always possible to apply this criterion given available data. When distinguished, both climbing up and climbing down were included as climbing. The following sections give more detail on behavioral data for taxa other than the Taï species.

Papio hamadryas cynocephalus The primary source here is Rose (1977), who reported results of a relatively short (one month) field study of *P. hamadryas anubis* near Gilgil, Kenya, in an area characterized mainly by open meadow with some mixed scrub and trees, as well as cliffs. The skeletal structural data in the present study were derived from a population of *P. h. cynocephalus* (Table 1), collected between Kibwesi and Darajani, Kenya by the National Museums of Kenya (Ruff, 2002). This is in an area of geographic overlap and probable hybridization between *P. h. cynocephalus* (yellow baboons) and *P. h. anubis* (olive baboons; Newman et al., 2004). These genetic analyses demonstrated a very close relationship between Kenyan populations of olive and yellow baboons, with data for yellow baboons collected near Darajani, in the same area that the present study skeletal specimens were derived. In addition, the general habitats in the areas where behavioral and morphological data were obtained are similar, both being characterized by open or semiopen environments of savanna or desert shrub and grass (Kenya Agricultural and Cash Crops, 1974; Winder, 2014). Thus, the behavioral data collected by Rose (1977) should be reasonably representative of the population from which the skeletal data were derived.

Percentages of time observed climbing and leaping were very low in Rose's (1977:Table 1) study, with climbing recorded at 0.7%.

Table 1
Sample sizes and frequencies (%) of total locomotor behavior.

Species	Abbr.[a]	n	Leaping	Climbing	Reference
Cercopithecus petaurista	C.p	3	10.1	18.8	McGraw (2000)
Cercopithecus campbelli	C.c	3	5.2	14.5	McGraw (1998)
Cercopithecus diana	C.d	6[e]	10.4	19.4	McGraw (1998)
Cercocebus atys	C.a	11[e]	1.0	12.5	McGraw (1998)
Papio h. cynocephalus[b]	Pap.c	20	0.5	1.5	Rose (1977)
Macaca nemestrina	M.n	9[e]	2.5	–	Caldecott (1986)
Macaca fascicularis	M.f	20	7.9	7.5	Cant (1988)
Colobus guereza	Col.g	18	38.0	8.4	Gebo and Chapman (1995)
Colobus polykomos	Col.p	8[e]	14.5	14.3	McGraw (1998)
Piliocolobus badius	Pil.b	41[e]	17.8	17.0	McGraw (1998)
Procolobus verus	Pro.v	3	20.4	12.0	McGraw (1998)
Trachypithecus cristatus[c]	T.c	10	30.0	12.1	Fleagle (1978)
Presbytis rubicunda[d]	P.r	10	53.6	13.7	Fleagle (1978)

[a] Species abbreviations used in Figures 3 and 4.
[b] Locomotor data based on *Papio hamadryas anubis* (see text).
[c] Locomotor data based on *Trachypithecus obscurus* (see text).
[d] Locomotor data based on *Presbytis melalophus* (see text).
[e] Samples sizes smaller for some analyses.

This included non-movement periods; as a percentage of locomotor behavior this rises to 2.8%. Leaping was recorded as an event, with 183 leaps observed in 7098 min. However, all of these observations combined all sex-age classes, and it was noted that both climbing and leaping were much more common among younger individuals. In fact, no leaps at all were recorded for adult animals (although they were observed to leap outside of recording periods), and about half of all climbing occurred during play sequences. Thus, the frequency of climbing in adults is estimated here as 1.5%, and the frequency of leaping as a nominal 0.5%. Hunt (1992) reported frequencies of climbing and leaping for olive baboons at Gombe, in a more forested environment, of 2.0% and 0.8% of total movement, respectively (our calculations from data in his Table 1), only slightly higher than our estimates.

Macaca fascicularis The primary source here is Cant (1988:Table 1), who recorded behavior as a percentage of distance moved. Percentages within 'traveling', 'foraging', and 'feeding' categories were combined by multiplying them by the total number of meters for each category, summing, and dividing by the total pooled number of meters. Leaping constituted 7.9% of total locomotion. Climbing (7.5%) included vertical climbing ("movement along a continuous vertical substrate, either upward or downward") and vertical clambering ("movement across or through multiple substrates in a vertical direction, either upward or downward"; Cant, 1988:31). Another qualitative source of information on locomotor behavior in *Macaca fascicularus* was provided by Rodman (1979:52), who noted that "Arboreal habits require *M. fascicularis* to leap between tree crowns relatively frequently and to travel on oblique supports that entail constant climbing up and down". This assessment broadly agrees with Cant's (1988) observations. Rodman (1979:52) also hypothesized that *M. fascicularis* "is expected to show structural adaptations indicating strength for climbing and leaping", relative to the less arboreal *M. nemestrina* (also see below).
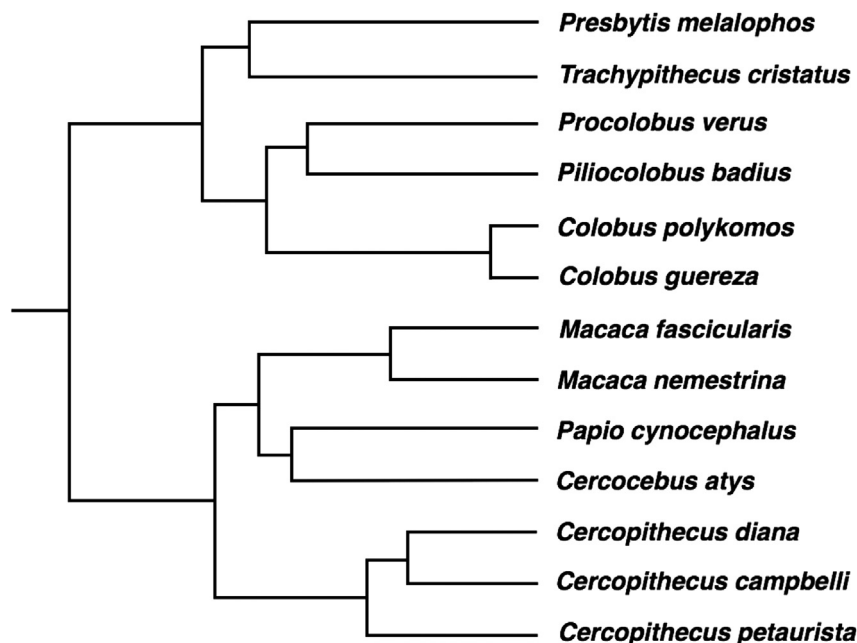

Figure 1. Consensus tree for the 13 species included in the present study, derived from the 10kTrees website (Arnold et al., 2010). Note that data were not available for *Presbytis rubicunda*; *Presbytis melalophus* (also used for locomotor data) was substituted. *Cercocebus atys* = *Cercocebus torquatus atys*; *Papio cynocephalus* = *Papio hamadryas cynocephalus*.

Macaca nemestrina The only available quantitative observations of locomotor behavior in *M. nemestrina* are those of Caldecott (1986). Using 'spot observations', he reported frequencies of 2.5% 'jumping' and 34.6% 'climbing' during 'foraging' (Caldecott, 1986:Table XVIII). While the relatively low frequency of leaping (jumping) matches with other observations for this taxon, the frequency of climbing seems extraordinarily high when compared with that of other species and qualitative assessments of this taxon by other observers. Fleagle (1980) considered *M. nemestrina* to be the most terrestrial of Malayan primates, exhibiting less climbing and leaping behavior than *M. fascicularis*. Rodman (1979) also noted the less frequent climbing and leaping of *M. nemestrina* and their more frequent long-distance terrestrial travel (although they fed in the trees). Other investigators have commented on the largely terrestrial nature of adult *M. nemestrina* (e.g., Ruppert et al., 2018). Caldecott (1986) did not define 'climbing' in his study, and it is possible that he included all arboreal behaviors (including more horizontally oriented movements) within this category. In addition, all age groups were apparently combined, which would inflate climbing frequency (juvenile *M. nemestrina* spend more time in trees than adults, according to substrate data reported by Caldecott, 1986 and behavioral observations by Ruppert et al., 2018). Study conditions may also have influenced Caldecott's (1986) results: the animals were never fully habituated and remained "very shy and elusive" even after a year of study (Caldecott, 1986:21), suggesting that they may have been more arboreal as an avoidance defense mechanism. Caldecott (1986:106) himself commented that his study groups tended to be more arboreal than in other reports for this species, and were "relatively slow moving or static when on the ground", which does not match with other descriptions of their behavior (e.g., Rodman, 1979). Because of these uncertainties, in the present study *M. nemestrina* was not included in analyses of climbing behavior.

Colobus guereza The primary behavioral source is Gebo and Chapman (1995:Table 11). Leaping (38.0% of total locomotion) was defined similarly to Fleagle (1977, 1978) and McGraw (1998). Gebo and Chapman (1995:Table 3) defined climbing as "movements which generally require greater mobility in the limbs; a movement up or down a vertical or steeply inclined support or through irregular and intertwined small supports (clambering, Cant, 1988); all four limbs move in an irregular pattern with abducted arms and knees and with variable hand and foot positions; the arms are used to pull the animal while the legs alternately push the body upward/forward". In order to limit this category to more vertical movements only (i.e., ≥45° from the horizontal), information on substrate orientation given in their Table 13 was utilized. 'Vertical' (75—90°, 9% of total climbing behavior) was combined with half of 'oblique' (15—75°, 80% of total climbing behavior) climbing to arrive at 49% of total climbing behavior, which was multiplied by 15% (all climbing as a percentage of all locomotion) to arrive at 7.4% of total movement. 'Bimanualism ("a movement in which the hands grasp a support and are used to pull the body up to a support from below", 1% of all movement) was also included in climbing, while 'vertical bounding' ("short successive jump-clings") was not (Gebo and Chapman, 1995:Table 3). Animals were judged to be "relatively well habituated to observers", although "still wary", possibly biasing canopy height data (Gebo and Chapman, 1995:51).

Morbeck (1977) reported similar results for leaping (34.5% of total locomotion) and a higher value for climbing (17.6%) in *C. guereza*, although climbing included non-vertical movements. All 'climbing' plus 'bimanualism' in Gebo and Chapman (1995) totaled 16% of total locomotor behavior, very similar to Morbeck's (1977) total figure. Rose (1979:Tables 4 and 5) reported lower values for leaping (19.6%) and higher values for climbing ('climb up': 20.9%; 'climb down': 15.6%) in *C. guereza*. 'Climbing' included movement at somewhat lower angles to the horizontal (to 30°). Unlike Gebo and Chapman (1995) and Morbeck (1977)—as well as McGraw (1998) and Fleagle (1978)—Rose (1979) recorded data as percentage of time rather than percentage of bouts observed, assigning an arbitrary 1 s period to leaps, which would tend to underestimate leaping percentage relative to other studies. Because climbing is a relatively slow activity, this might also overestimate climbing relative to percentage of locomotor bouts. Issues related to different behavioral recording methods are further addressed in the Discussion. Mittermeier and Fleagle's (1976:243) qualitative description of locomotion in *C. guereza* noted that leaping is "very common".

Trachypithecus cristatus and *Presbytis rubicunda* Locomotor data for these species were obtained from Fleagle (1978:Table 1) through analogy with the closely related taxa *Trachypithecus obscurus* (formerly in *Presbytis*) and *Presbytis melalophos*, respectively. Environmental conditions (relatively undisturbed tropical rainforest) were similar for the behavioral field site (in Selangor State, Malaysia; Bernstein, 1968) and the source location for the *T. cristatus* and *Pr. rubicunda* skeletal material analyzed here (Sabah State, Malaysia; Anonymous, 1937). Fuentes (1996), citing Davies (1984), noted that locomotor patterns of *Pr. rubicunda* are very similar to those of *Pr. melalophos* in Malaysia. Definitions employed by Fleagle (1977, 1978) for leaping and climbing were given earlier. Leaping included 'hops' ("a series of consecutive leaps"; Fleagle, 1977:298). As noted, climbing included both vertical and more horizontal movements (potential effects of this difference on study results are considered later). Data for traveling and feeding, obtained through bout sampling, were combined by multiplying percentages of observed bouts by the total number of bouts within each category, then calculating a percentage over both categories.

2.2. Bone structural parameters

Linear articular dimensions of the femur and humerus were measured with digital calipers as described and illustrated previously (Ruff, 2002). They included superoinferior (S-I) and anteroposterior (A-P) breadths, and depths of the femoral and humeral head articular surfaces, as well as mediolateral (M-L) breadth of the distal femoral and humeral articular surfaces. These dimensions and other dimensions calculated from them (see below) were originally defined (Ruff, 2002) with reference to hominoid articulations; for the humeral head in cercopithecoids, 'A-P' breadth is actually taken mediolaterally, across the mediolaterally widest portion of the articular surface. S-I breadth is taken from the most superior to most inferior points on the articular surface, parallel to the lateral margin of the surface, approximated by a straight line. Femoral and humeral head articular surface depths are taken perpendicular to the same lateral margin (Ruff, 2002:Appendix 1, Fig. 1)—as viewed anteriorly in the femur, and laterally in the humerus for cercopithecoids. A-P breadth and depth were used in combination with S-I breadth and geometric formulae for partial spheres to calculate femoral and humeral head articular surface areas (Ruff, 2002: Appendix 1, Table 1). M-L breadth of the distal femoral articular surface is taken at the most posteriorly projecting points of the condyles, and M-L breadth of the distal humeral articular surface across the middle of the surface, parallel to the trochlear-capitular M-L axis (also see Perry et al., 2018:Fig. 1). These breadths, and S-I breadths of the femoral and humeral heads, were used as measures of overall joint size.

We were able to compare surface areas of the humeral head calculated using the geometric model (Ruff, 2002) with those

determined from laser scans in 21 individuals from the Taï samples (4 *Cercopithecus diana*, 5 *Cercopithcus atys*, 6 *Colobus polykomos*, and 6 *Piliocolobus badius*) included in this study and a previous study (Dunham et al., 2017). A scatterplot showing results of the comparison is given in Figure 2. The correlation between the two estimates is r = 0.95, with a %SEE of 4.4%. The mean difference between values is 0.6%, and all individual values are within 8%. Mean deviations for all four species are within 4%. Thus, despite some approximations involved in geometric modeling, this method of estimating articular surface areas appears to give reliable results, similar to previously reported comparisons (Godfrey et al., 1995; Rafferty, 1996; Ruff, 2002).

Cross-sectional diaphyseal dimensions were obtained using ordinary medical CT for specimens previously reported (Ruff, 2002), and peripheral quantitative CT (pQCT; Ferretti et al., 1996; Schiessl et al., 1996) for the Taï specimens. Specimens were first aligned according to previously defined global axes, and a bone length dimension referred to as length' determined; length' is measured from the condyles to the superior surface of the femoral neck, and from the lateral lip of the trochlea to the superior surface of the humeral head (Ruff, 2002). Cross-sectional images were then obtained at 50% of length' in the femur, and at 40% of length', measured from the distal end, in the humerus (to avoid the deltoid tuberosity).[1] For the previously studied specimens, cross-sectional structural properties were determined using external software (see Ruff, 2002). For the Taï specimens, the internal software of the pQCT system (XCT Research SA+) was used.

The geometric section property that we focused on here was the polar section modulus, Z_p, of the femur and humerus. Z_p is an index of torsional strength and (twice) average bending strength. In very non-circular sections Z_p overestimates true torsional strength (Daegling, 2002), but all of the sections here were relatively round. It is thus a good overall measure of diaphyseal strength and has been used in several recent analyses of inter-limb bone strength proportions in nonhuman primates (Ruff et al., 2013, 2018a; Sarringhaus et al., 2016). The pQCT software calculates true polar section moduli, determined as the polar second moment of area divided by the maximum distance from the centroid to the subperiosteal surface. In the previous study of the non-Taï specimens included here (Ruff, 2002), section moduli were approximated by dividing second moments of area by A-P and M-L radii. These section moduli were corrected to true section moduli here by calculating conversion formulae based on the Taï specimens, using second moments of area and A-P and M-L breadths measured on the Taï sample to replicate the older method (r = 0.995–0.995, percent standard errors of estimate [%SEE] = 3.0–3.4%, n = 62–77).

2.3. Statistical analyses

Following previous analyses (Ruff, 2002; Ruff et al., 2013, 2018a; Sarringhaus et al., 2016), variation in inter- and intra-limb proportions was evaluated using (natural) log ratios of structural parameters. These include ratios of femoral to humeral Z_p, femoral and humeral head surface areas to their respective diaphyseal Z_p values, femoral to humeral head surface areas, and femoral to humeral proximal and distal articular breadths (Table 2). To compare with locomotor frequencies, species means of these log ratios were

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[1] Use of the 40% rather than midshaft section of the humerus follows a number of other comparative studies (Ruff, 2002, 2003a; Ruff et al., 2013, 2018a; Sarringhaus et al., 2016). In addition to avoiding the localized effects of variation in entheseal morphology associated with the deltoid tuberosity, this also samples a section closer to the minimum bending strength of the humerus, which has some advantages when predicting maximum load carrying capacity (e.g., see Campione and Evans, 2012).
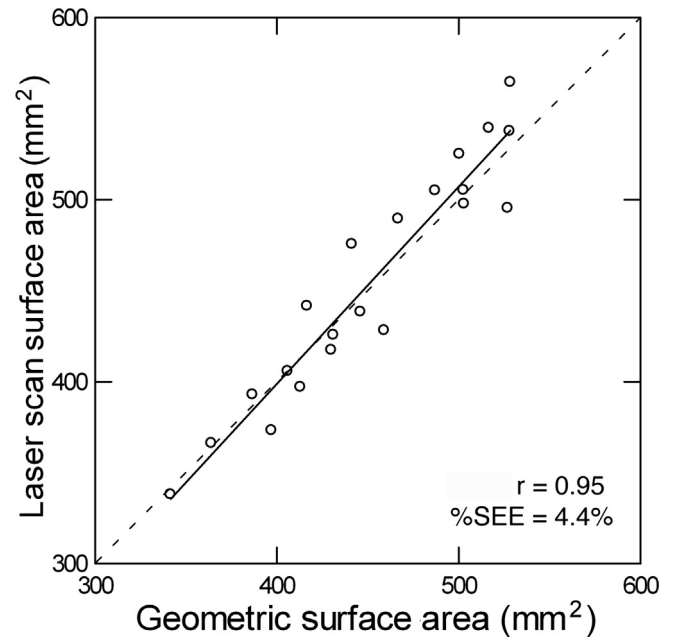

Figure 2. Surface area of the humeral head determined through laser scanning versus through linear measurements and geometric modeling in four cercopithecid species. Solid line: least squares regression; dashed line: equivalence.

calculated. No variable in any species departed significantly from normality ($p \leq 0.05$, Shapiro–Wilks and Anderson-Darling tests), except marginally for humeral head surface area to diaphyseal Z_p in *Ce. diana* ($p = 0.032-0.036$) and femoral head surface area/diaphyseal Z_p in *C. guereza* ($p = 0.045-0.060$), and even in these cases, mean and median values were very close (within 5%).

Possible phylogenetic effects on the relationship between locomotor behavior and bone structural ratios were evaluated using a phylogenetic generalized least squares (PGLS) regression model, employing the maximum likelihood estimate of Pagel's λ (Pagel, 1999). The consensus tree for the 13 species included in the present study was obtained from the 10kTrees website (Arnold et al., 2010) and is shown in Figure 1. The PGLS regression analysis was carried out using the R packages ape and caper (Paradis et al., 2004; R Core Team, 2013)

As shown in Table 2, almost all relationships show a strong phylogenetic effect, i.e., λ = 1. The main exception is leaping and FZ_p/HZ_p, which has a λ of 0, i.e., there is no discernible phylogenetic effect on the relationship between leaping and femoral to humeral diaphyseal strength. Leaping and femoral to humeral distal articular breadth (FDML/HDML) shows only a weak phylogenetic effect,

Table 2
Results of phylogenetic generalized least squares analyses.

Proportion	Leaping			Climbing		
	λ	p 0	p 1	λ	p 0	p 1
$\ln(FZ_p/HZ_p)$	0	1	0.0036	1	0.0826	1
$\ln(FHSA/FZ_p^{.667})$	1	0.2634	1	1	0.1474	1
$\ln(HHSA/HZ_p^{.667})$	1	0.0736	1	1	0.0312	1
$\ln(FHSA/HHSA)$	1	0.1663	1	1	0.1080	1
$\ln(FHSI/HHSI)$	1	0.0266	1	1	0.0105	1
$\ln(FDML/HDML)$	0.296	0.7346	0.1443	1	0.2913	1

Abbreviations: FZ_p = femoral diaphyseal strength; FHSA = femoral head surface area; FHSI = femoral head superoinferior breadth; FDML = femoral distal articular mediolateral breadth; HZ_p = humeral diaphyseal strength; HHSA = humeral head surface area; HHSI = humeral head superoinferior breadth; HDML = humeral distal articular mediolateral breadth.

with λ closer to 0 (0.296) than to 1. Following these results, regressions and correlations between leaping and climbing frequencies and structural proportions were carried out after correcting for phylogenetic non-independence, using the same statistical routines given above.

Because body size may also affect locomotor behavior (e.g., Fleagle and Mittermeier, 1980), we also carried out phylogenetically controlled analyses including body mass as a covariate (species average body masses were obtained from individually associated values (Ruff, 2002) or sex-species averages for the Taï samples (Oates et al., 1990). However, in no case was body mass a significant or near-significant factor contributing to associations between locomotor frequencies and structural proportions ($p > 0.10$, all analyses). This is consistent with previous behavioral studies for Old World monkeys, which have shown little if any association between leaping and climbing frequencies and body mass (Gebo and Chapman, 1995; McGraw, 1998). Thus, body mass was not included in subsequent analyses.

3. Results

Species mean structural proportions used in subsequent analyses are given in Table 3, along with within-species sample sizes included each analysis. All individual raw data are listed in Supplementary Online Material (SOM) Table S1.

Phylogenetically-controlled correlations between structural proportions and frequency of leaping and climbing are given in Table 4. Scatterplots and phylogenetically-controlled least squares regressions are shown in Figures 3 and 4 (leaping and climbing, respectively). The strongest structural-behavioral correlation ($r^2 = 0.781$) is between leaping and the ratio of femoral to humeral Z_p (Fig. 3a). Ratios of femoral to humeral articular breadths and surface areas are also positively correlated with leaping (Fig. 3d—f), although less strongly than diaphyseal strength (Table 4). The femoral/humeral head surface area ratio has a lower correlation with leaping than the two articular breadth ratios. Articular surface area relative to diaphyseal strength in either the humerus or femur is not significantly correlated with leaping (Table 4; Fig. 3b,c).

Femoral/humeral diaphyseal strength is uncorrelated with climbing frequency (Table 4; Fig. 4a). Articular surface area/diaphyseal strength of the humerus is positively correlated with climbing ($r^2 = 0.502$; Fig. 4c); however, the same ratio in the femur shows a weaker negative correlation with climbing ($r^2 = 0.392$; Fig. 4b). As a result, femoral to humeral head surface area has a

Table 4
Correlations between bone structural properties and locomotor behavior (phylogenetically controlled).

Proportion	Leaping		Climbing	
	R^2	p	R^2	p
Ln(FZp/HZp)	0.781	<0.001	0.0003	0.96
Ln(FHSA/FZp^.667)	0.096	0.30	0.392	0.03
Ln(HHSA/HZp^.667)	0.093	0.31	0.502	0.01
Ln(FHSA/HHSA)	0.403	0.02	0.685	<0.001
Ln(FHSI/HHSI)	0.583	0.002	0.310	0.06
Ln(FDML//HDML)	0.568	0.002	0.069	0.41

Abbreviations: FZ_p = femoral diaphyseal strength; FHSA = femoral head surface area; FHSI = femoral head superoinferior breadth; FDML = femoral distal articular mediolateral breadth; HZ_p = humeral diaphyseal strength; HHSA = humeral head surface area; HHSI = humeral head superoinferior breadth; HDML = humeral distal articular mediolateral breadth.

strong negative association with climbing ($r^2 = 0.685$; Fig. 4d). Femoral to humeral articular breadth ratios are only near-significantly ($p < 0.06$; proximal) or non-significantly (distal) correlated with climbing frequency (Fig. 4e,f).

4. Discussion

Based on previous comparisons among catarrhines more generally, we predicted that locomotor behavior in our 13 cercopithecid species would be associated with systematic differences in diaphyseal and articular proportions of the femur and humerus. Specifically, we predicted that femoral to humeral proportions for diaphyseal strength and articular dimensions would be increased in more frequent leapers, and articular dimensions would be increased relative to diaphyseal strength in more frequent climbers, with articular surface area proportions more strongly related to climbing (due to their more direct effects on joint excursion) and articular breadths to leaping (because they reflect joint size and are less directly related to excursion). Most of the study predictions were supported by our results, although there were also some unexpected findings. Results are considered by locomotor category below, followed by more general considerations.

4.1. Leaping

Femoral to humeral diaphyseal strength is very strongly positively correlated with frequency of leaping, as predicted. This relationship is apparently similar in both cercopithecines and colobines:

Table 3
Species mean bone structural proportions and variable-specific sample sizes within parentheses.

Species	Proportion					
	ln(FZp/HZp)	ln(FHSA/FZp^.667)	ln(HHSA/HZp^.667)	ln(FHSA/HHSA)	ln(FHSI/HHSI)	ln(FDML/HDML)
Cercopithecus petaurista	0.340 (3)	2.550 (3)	2.848 (3)	−0.071(3)	−0.175(3)	0.294 (3)
Cercopithecus campbelli	0.299 (3)	2.663 (3)	2.899 (3)	−0.036 (3)	−0.163 (3)	0.249 (3)
Cercopithecus diana	0.389 (4)	2.628 (6)	2.978 (4)	−0.097 (4)	−0.162 (4)	0.248 (4)
Cercocebus atys	0.399 (5)	2.583 (10)	2.737 (5)	0.098 (5)	−0.103 (5)	0.243 (5)
Papio cynocephalus	0.288 (20)	2.679 (20)	2.434 (20)	0.437 (20)	−0.056 (20)	0.273 (20)
Macaca nemestrina	0.242 (8)	2.572 (9)	2.734 (8)	0.034 (8)	−0.084 (8)	0.236 (8)
Macaca fascicularis	0.451 (20)	2.643 (20)	2.677 (20)	0.267 (20)	−0.087 (20)	0.287 (20)
Colobus guereza	0.544 (18)	2.701 (18)	2.680 (18)	0.384 (18)	−0.017 (18)	0.303 (18)
Colobus polykomos	0.489 (4)	2.618 (8)	2.762 (6)	0.189 (4)	−0.077 (4)	0.282 (4)
Piliocolobus badius	0.391 (30)	2.551 (41)	2.677 (35)	0.126 (31)	−0.085 (31)	0.207 (31)
Procolobus verus	0.490 (3)	2.493 (3)	2.692 (3)	0.127 (3)	−0.109 (3)	0.252 (3)
Trachypithecus cristatus	0.444 (10)	2.477 (10)	2.404 (10)	0.369 (10)	0.020 (10)	0.303 (10)
Presbytis rubicunda	0.765 (10)	2.530 (10)	2.559 (10)	0.482 (10)	0.075 (10)	0.398 (10)

Abbreviations: FZ_p = femoral diaphyseal strength; FHSA = femoral head surface area; FHSI = femoral head superoinferior breadth; FDML = femoral distal articular mediolateral breadth; HZ_p = humeral diaphyseal strength; HHSA = humeral head surface area; HHSI = humeral head superoinferior breadth; HDML = humeral distal articular mediolateral breadth.
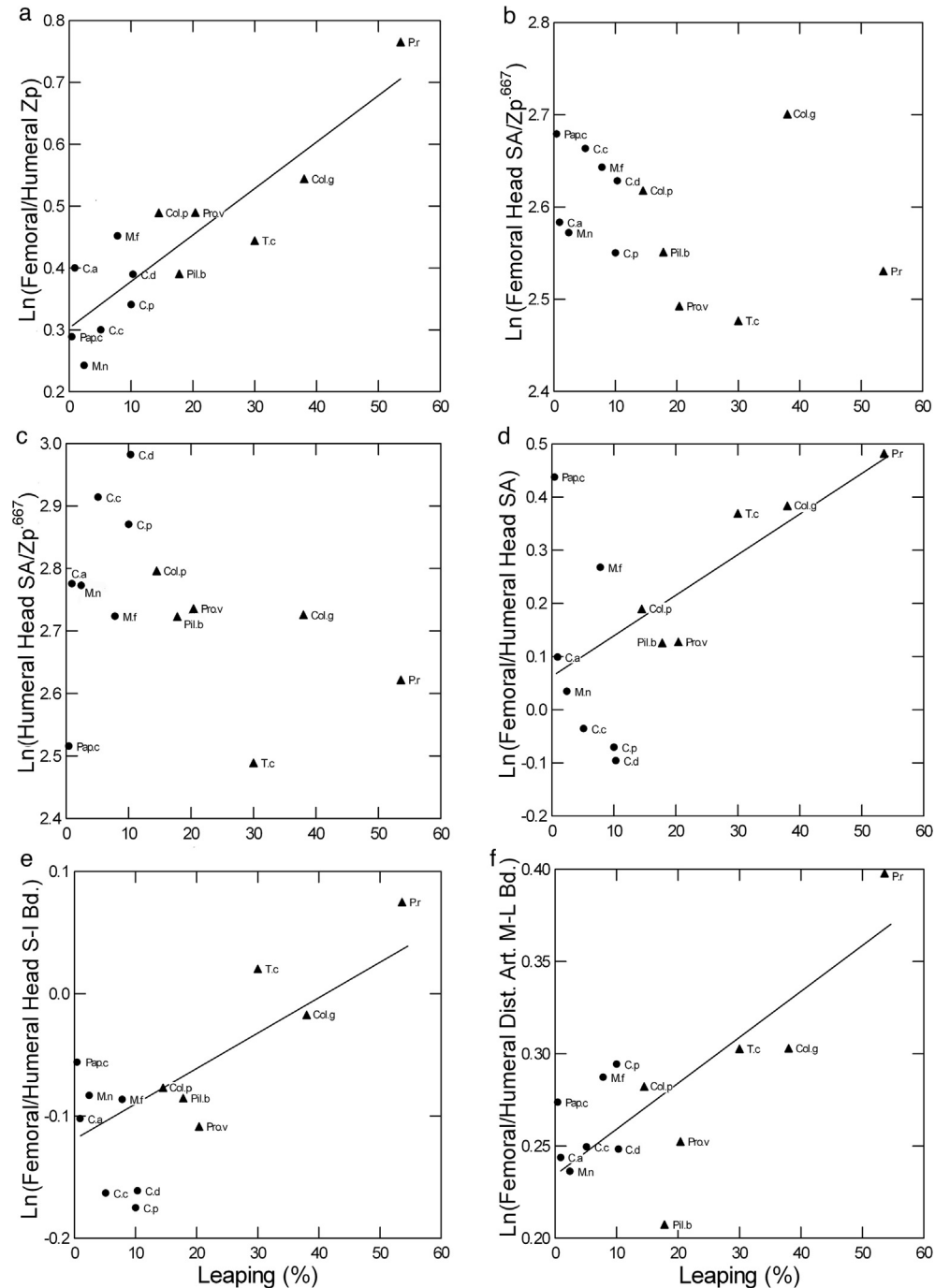
Figure 3. Scatterplots of bone structural proportions against leaping frequencies, based on data in Tables 1 and 3, with phylogenetically-controlled regressions (no line plotted where $p > 0.05$): a) femoral/humeral diaphyseal strength; b) femoral head surface area/diaphyseal strength; c) humeral head surface area/diaphyseal strength; d) femoral/humeral head surface area; e) femoral/humeral head superoinferior breadth; f) femoral/humeral distal articular mediolateral breadth. Filled circles = cercopithecines; filled triangles = colobines. Symbols labeled with genus and species first letters, except in cases of possible confusion, where first three letters of genus are given. See Tables 1 and 3 for list of taxa, Table 1 for taxa abbreviations, and Table 3 for explanation of structural properties.

separate regression lines plotted through the two groups are virtually colinear (SOM Fig. S1). The results of the PGLS regressions, showing no phylogenetic influence on the relationship, also support this inference. Thus, the functional signal of relative strengthening of the femur in leapers outweighs any phylogenetic effect.

The physical basis for increased bending/torsional loads on the hind limb during leaping is relatively straightforward. In all of the behavioral studies used here (where specifically described),

'leaping' involved propulsion of the body primarily generated by the hind limbs, resulting in horizontal movement across substrate gaps, and did not include purely vertical 'dropping'. Leaping generates very high peak substrate reaction forces when compared to quadrupedal walking and running (Demes et al., 1999). Although the forelimbs are used for braking during landing, take-off forces are higher, at least on compliant surfaces (Demes et al., 1999). It should be noted that these experimental results were obtained for
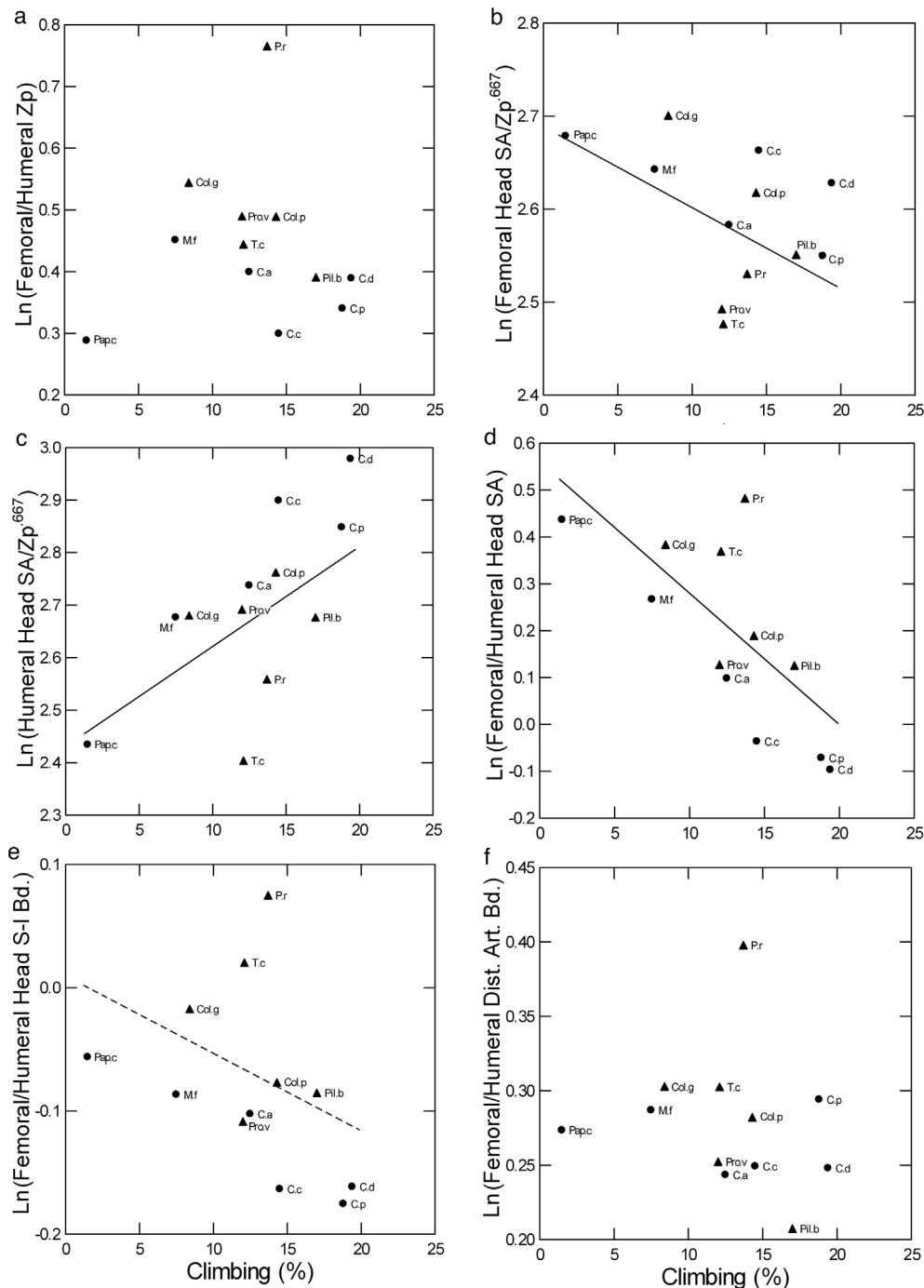
Figure 4. Scatterplots of bone structural proportions against climbing frequencies, with phylogenetically-controlled regressions (no line plotted where $p > 0.05$, except in e [dashed line], where $p = 0.069$): a) femoral/humeral diaphyseal strength; b) femoral head surface area/diaphyseal strength; c) humeral head surface area/diaphyseal strength; d) femora/humeral head surface area; e) femoral/humeral head superoinferior breadth; f) femoral/humeral distal articular mediolateral breadth. See Tables 1 and 3 for list of taxa, Table 1 for taxa abbreviations, and Table 3 for explanation of structural properties. Symbols as in Figure 3.

strepsirrhines, not anthropoids, so are not directly transferable to the present study taxa. Still, it is likely that the same general principles apply, at least in terms of relative comparisons between different anthropoid taxa.

Bone (limb) length also likely affects bending loads on long bone diaphyses by increasing muscular and gravitational force moment arms (Selker and Carter, 1989; Polk et al., 2000; Ruff, 2000). As would be expected (Emerson, 1985), femoral to humeral maximum length does show a strong relationship to leaping frequency in the present study sample ($r^2 = 0.629$, $p = 0.001$), although not as strong as femoral to humeral Z_p ($r^2 = 0.781$). Thus, it is possible that phylogenetic effects on relative limb length could contribute to the observed patterning in diaphyseal strength proportions. However, PGLS regression indicates no phylogenetic effect on the relationship of femoral/humeral length to leaping in this sample ($\lambda = 0$, probability $0 = 1$, probability $1 = 0.122$). Furthermore, the regression of femoral/humeral Z_p on leaping frequency with femoral/humeral length as a covariate is still significant ($p = 0.014$).

This is not to say that there are no phylogenetic associations of femoral/humeral strength (or length) proportions: colobines generally have relatively stronger (and longer) femora, consistent with their higher frequencies of leaping (Fig. 3). Similar results have been reported by O'Neill and Dobson (2008). However, the relationship between diaphyseal strength proportions and leaping behavior is not affected by phylogeny, at least within the present study sample. This is consistent with the observed developmental plasticity of diaphyseal cross-sectional proportions in response to changes in mechanical loading, again, relatively independently of changes in bone length proportions (Ruff, 2003b; Sarringhaus et al., 2016; Ruff et al., 2018a). This does not argue for an absence of genetic effects on bone structural proportions, of course—for example, some differences in proportions between taxa or populations within a taxon have been demonstrated to be present very early in development, prior to any significant locomotor loading (Cowgill, 2010; Young et al., 2018). Such adaptations argue for both genetic selection as well as direct environmental modification during development as contributors to final adult proportions.

As we also predicted, articular size is increased in the femur relative to the humerus in more frequent leapers in our sample. This can be attributed to a predicted increase in joint reaction forces (JRF) in the femur, following the same reasoning as above: a larger joint helps to reduce stress under increased loading. However, correlations are lower than with the diaphyseal strength proportion, and phylogeny has a strong effect on the relationship between leaping and relative articular size for the two proximal articular dimensions. This suggests that other mechanical and possibly historical factors also influence relative articular size. As shown earlier and discussed further below, relative articular size is associated with climbing frequency, which is not correlated with leaping frequency in our sample (r = 0.141, p = 0.65). Joint excursion is affected in particular by relative surface area, which depends upon extension of the surface in all three dimensions (Jenkins and Camazine, 1977; Rose, 1989; MacLatchy and Bossert, 1996; Hammond, 2014). Thus, assuming some variation in joint excursion unrelated to leaping frequency, we also predicted that femoral/humeral articular surface area would be less highly correlated with leaping than femoral/humeral articular breadth, which is less directly related to joint excursion. This was also found to be the case in our sample. This finding is consistent with results of an earlier study of body mass prediction, where limb bone articular breadths were more highly correlated with body mass (which is also related to JRF) than were articular surface areas in catarrhines as a whole, and within hominoids and cercopithecoids (Ruff, 2003a).

Almost all proportions involving articulations showed strong phylogenetic effects on their relationship to leaping (and climbing). This may reflect in part the apparently greater genetic canalization of articular compared to cross-sectional diaphyseal morphology (Trinkaus et al., 1994; Lieberman et al., 2001; Ruff et al., 2018a). The only exception to this pattern was femoral to humeral distal articular M-L breadth. Because the knee is a modified hinge joint, variation in M-L breadth has little effect on joint excursion, and thus locomotor capabilities. This may explain why transverse dimensions of the knee joint relative to body mass show very little variation within catarrhines and platyrrhines (Ruff, 2003a; Perry et al., 2018). Mediolateral breadth of the distal humeral articular surface relative to body mass does show phylogenetic patterning (Perry et al., 2018), possibly in relation to variation in pronation/supination capabilities as well as stabilization of the elbow joint throughout flexion and extension (Rose, 1993). The small degree of phylogenetic effect on knee/elbow M-L breadth in relation to leaping may in part result from the invariance of knee breadth (relative to body mass) across taxa combined with some phylogenetic effects on relative elbow breadth.

Articular surface area relative to diaphyseal strength of either the femur or humerus was not correlated with leaping frequency. This follows from the above results, where both joints and shafts of the hind limb long bones should be subject to greater forces in leapers; thus, intralimb proportions should not vary greatly in relation to leaping. Except for one outlier (C. guereza), there was a visual tendency for femoral head surface area/diaphyseal strength to show some decline with increased frequency of leaping, however (Fig. 3b; the negative correlation is significant [p = 0.03] without this taxon). This weak tendency is likely a result of the more consistent positive effect of leaping on femoral diaphyseal strength.

4.2. Climbing

Humeral head articular surface area relative to diaphyseal strength was greater in more frequent climbers, as predicted. This follows generally from previous morphological observations and predicted greater shoulder excursion in movements involving reaching, abduction, and elevation of the arm (Rose, 1989; Larson, 1993; but see Chan, 2007, 2008). The correlation would have been even stronger except for the low outlier positions of Pr. rubicunda and particularly T. cristatus, i.e., they have lower ratios than would be predicted for their climbing frequencies (Fig. 4c). As noted earlier, 'climbing' for these taxa included more horizontal as well as vertical movements, which would have inflated climbing percentages relative to other taxa. Using Gebo and Chapman's (1995) data for C. guereza as a guide, only about half of their original total 'climbing' category, which appears similar to that employed by Fleagle (1978) for Trachypithecus and Presbytis, was actually vertical climbing (see above). If this same adjustment (dividing in half) to climbing frequency is made here for Trachypithecus and Presbytis, the correlation between humeral head surface area/diaphyseal strength and climbing over all taxa rises from an r^2 of 0.502 to an r^2 of 0.677 (p = 0.001), almost as high as that between leaping and femoral/humeral diaphyseal strength. Thus, this appears to be a relatively strong relationship.

Unexpectedly, femoral head surface area relative to femoral diaphyseal strength showed a moderate negative correlation with climbing frequency ($r^2 = 0.392$). If the adjustments to climbing frequencies for T. cristatus and Pr. rubicunda are made, this falls to $r^2 = 0.190$, which is nonsignificant (p = 0.16). Regardless, it is apparent that, unlike in the humerus, femoral head surface area does not increase relative to shaft strength among more frequent climbers in the study sample. This is also unlike the pattern found among catarrhines generally, where nonhuman hominoids have increased femoral head surface area relative to diaphyseal strength compared to cercopithecoids (Ruff, 2002). This was interpreted to reflect the frequent use of abducted hip postures in hominoids during climbing and quadrumanous clambering, and is particularly marked in hominoids who engage most frequently in these behaviors—Pongo and Symphalangus syndactylus (Fleagle, 1976a; Cant, 1987; Isler, 2005; Neufuss et al., 2017).

Hunt (1992) considered the kinematics of climbing in chimpanzees and baboons at Mahale and Gombe to be similar; however, he focused primarily on torso and forelimb positioning and did not report on degree of hip abduction or foot positioning. Forelimb positioning was also different between the species when climbing on large diameter supports, suggesting different kinematics in this situation. More recent studies indicate that vertical climbing in hominoids can involve considerable shoulder abduction and forelimb elevation (Isler, 2005; Neufuss et al., 2017), and that "the purported similarity between hominoids and cercopithecoids in vertical climbing kinematics must be strongly questioned" (Isler, 2005:77). Aside from reports on sagittal plane motions in Macaca fuscata and M. fascicularis (Hirasaki et al., 1993; Hanna and Schmitt,

2011), no quantitative data on limb positioning in cercopithecoids during climbing are, to our knowledge, available. However, foot and ankle structure within cercopithecoids in general, regardless of degree of arboreality, allows less mobility than in hominoids, and is highly conserved (Gebo, 1993; DeSilva, 2008), possibly as a result of a common terrestrial or semiterrestrial ancestry (Strasser, 1988; Gebo, 1989, 1993; Meldrum, 1989; Benefit, 1999). This in turn suggests that lower limb positioning during climbing may be broadly similar in all cercopithecoids, at least in comparison to hominoids, and involve less foot inversion and hip abduction (although subtle differences in foot structure between cercopithecines and colobines may be related to generally increased arboreality in colobines; Strasser, 1988). Experimental in vivo manipulation of hip joints does indeed show similarity between colobines and cercopithecines in range of abduction, with all falling below hominoids (Hammond, 2014).[2] Thus, greater frequency of climbing behavior in cercopithecoids, unlike in hominoids, may not be facilitated by increased relative surface area of the femoral head.

Another factor in the disparity in results here with those for hominoids (Ruff, 2002) is that the femoral head surface area/diaphyseal ratio also depends on diaphyseal strength. In the previous study (also see Ruff, 1988), it was hypothesized that increased articular surface area relative to diaphyseal strength should be most evident in taxa characterized by both a high degree of joint mobility as well as relatively slow, cautious movement, which would decrease dynamic bending and torsional loads on the diaphyses. This was indeed largely borne out by the results of the previous study (Ruff, 2002), but may be less relevant to the current study taxa, none of whom would be categorized as cautious movers (although, as further discussed below, some move much more than others throughout the day). Therefore, both a limited range of variation in lower limb positioning during climbing, and a lack of association between climbing frequency and cautious movement, may explain the absence of a positive relationship between femoral head articular surface area/diaphyseal strength and increased climbing among cercopithecoids.

The combined negative trend in the femur and positive trend in the humerus for proximal articular surface area to diaphyseal strength results in a strongly negative trend in femoral/humeral head surface area relative to climbing frequency ($r^2 = 0.685$), which becomes even stronger if the adjustment to climbing frequency for *T. cristatus* and *Pr. rubicunda* is carried out ($r^2 = 0.861$, $p \ll 0.001$). The trend is clearly apparent in both cercopithecines and colobines, especially if this adjustment is made (Fig. 4d). A similar, but much weaker trend is apparent for femoral/humeral head S-I breadth ($r^2 = 0.310$, $p = 0.06$); this becomes significant with the adjustment for *T. cristatus* and *Pr. rubicunda* ($r^2 = 0.576$, $p = 0.004$), but is still far lower than that for surface areas. The correlation between climbing and distal femoral/humeral M-L articular breadth is very low, and remains nonsignificant with the adjustment for *T. cristatus* and *Pr. rubicunda*. Thus, proximal surface area proportions in particular appear to be diagnostic of climbing frequencies in cercopithecoids, due to the specific effects of climbing on relative surface area of the humeral head (but not femoral head).

Climbing frequency was not associated with femoral/humeral diaphyseal strength (this remains the case if the adjustment is carried out for *T. cristatus* and *Pr. rubicunda*). In comparisons among catarrhines in general, femoral/humeral diaphyseal strength is associated (negatively) with forelimb suspensory behavior as well as (positively) with leaping frequency (Ruff, 2002). Movement involving forelimb suspension, i.e., arm-swinging, was not observed or very rare among the present study taxa—the only taxa in which it was reported were *Pr. obscura*, at 2.7% of total locomotor behavior (Fleagle, 1978) and *Piliocolobus badius*, at 3.7% (McGraw, 1998); thus, it should not have been a significant factor in our analyses. Our results suggest that cercopithecoid-like climbing does not create relatively higher mechanical loadings on the forelimb, which seems consistent with the limited available qualitative and quantitative kinematic data (Hunt, 1992; Hirasaki et al., 1993). In contrast, intra- and interspecific structural analyses of chimpanzees and gorillas strongly suggest that increased frequency of climbing (and suspensory activities) results in relatively higher loads on the forelimb (Ruff et al., 2013, 2018a; Sarringhaus et al., 2016), consistent with general observations on the kinematics of climbing in hominoids (Isler, 2005; Neufuss et al., 2017).

4.3. Further considerations

Bone material properties Only geometric properties were used for assessment of diaphyseal strength here, not taking into consideration possible variation in material properties (stiffness, material strength, etc.) between bones or taxa, which could affect bone strength estimates. However, some information on material properties of the Taï specimens was available, since the pQCT scanner used for measuring them also calculates bone mineral density (BMD), which is strongly related to other material properties (Currey, 1984; Brear et al., 1990). A polar section modulus 'strength strain index' (SSI) that incorporates both geometric and mineral density distributions of material throughout a cross section (see Schiessl et al., 1996 for a more detailed description) is highly correlated ($r = 0.998$, %SEE = 2.6%) and virtually isometric (slope = 0.987, SE = 0.005) with the purely geometric polar section modulus used in the present study. This is consistent with other analyses that incorporated actual mechanical testing of whole bones, which showed very strong correlations between geometric properties and bone strength and rigidity, and little improvement in correlations when BMD distributions were also considered (Weatherholt and Warden, 2016). Thus, variation in geometry appears to be primary in determining variation in long bone diaphyseal strength, at least in similar skeletal elements (Erickson et al., 2002; Ruff et al., 2018b).

However, there is evidence that cortical bone mineral density may vary systematically between some taxa. On average, the Taï samples have higher bone mineral densities (mean = 1424 ± 38 (SD) mg/cm^3; species means range from 1397 to 1440 mg/cm^3) than reported previously for mammalian compact bone generally (about 1200 mg/cm^3; Gong et al., 1964), or what we obtained for seven (dry) human autopsy femora that we scanned using pQCT (1202 ± 38 mg/cm). Femoral and humeral bone BMD for two captive *Macaca mulatta* cadaveric specimens scanned using pQCT were very similar to those of the Taï specimens (1418 ± 18.2 mg/cm^3), suggesting that diagenesis is not responsible for the higher Taï values. Bone mineral densities measured in adult gorilla long bones, using the same pQCT scanner (Ruff et al., 2018a), were considerably lower on average: 1076 ± 37 ($n = 109$) and 1106 ± 36 ($n = 111$) mg/cm^3 for the femur and humerus, respectively. Differences between bones that had been collected after burial and those obtained from wild-shot (cadaveric) gorilla specimens were negligible (within a few percent), again arguing against variable

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[2] One of the two colobines measured in Hammond (2014), *Trachypithecus francoisi*, had a somewhat larger measured range of hip abduction (41°) than the other colobine species (*C. guereza*) or the three cercopithecines in her sample (*M. fascicularis, Macaca mulatta, Papio* sp.), all of which ranged between 24 and 28° (species means). However, the sample size for *T. francoisi* was only one individual, who was likely not skeletally mature (3.0 years of age; Bolter, 2011). Although ranges of hip extension and flexion do not change significantly in *M. mulatta* and *Erythrocebus patas* past the first year or two of life (Turnquist, 1983; Turnquist and Kessler, 1989), the effects of age on hip abduction was not tested in those studies, so may also have been a factor in producing this result.

preservation as an explanation.[3] Thus, based on this very limited sampling, at least some cercopithecoid taxa may have higher diaphyseal BMD than humans or gorillas. Whether there are any allometric effects on BMD (i.e., that smaller taxa have denser bones) requires more extensive sampling (there is no correlation between BMD and body mass among the Taï samples; $p > 0.50$ in both the humerus and femur).

Femoral cortical density is also slightly higher (1438 ± 30 mg/cm^3) than humeral cortical density (1413 ± 33 mg/cm^3; paired t test significant at $p < 0.001$) in the Taï specimens. There is no correlation between either femoral or humeral cortical density, or the ratio of femoral to humeral density, and leaping or climbing frequency among the Taï specimens ($p > 0.25$, all comparisons). In a histological comparison between Taï species with relatively high (*Colobus polykomos*, *Pi. badius*) and low (*Ce. diana*, *Cer. atys*) leaping frequencies, Lad et al. (2018) found greater osteon population density and percent Haversian bone in the femora of more frequent compared to less frequent leapers, but the same parameters were greater overall in humeri than in femora in both groups. Thus, results only partially fulfilled mechanical expectations, i.e., that more mechanically stressed bones would be more extensively remodeled. The slightly higher bone mineral density in femora compared to humeri in the present study is consistent with Lad et al.'s (2018) results, since remodeling (greater in humeri in their sample) leads to increased porosity and lower average mineralization of bone (Currey, 1959). In gorillas (Ruff et al., 2018a), femora are slightly but consistently ($p < 0.001$, paired t tests) less dense than humeri (see above). Whether these intra- and interspecies patterns are related to mechanical, systemic (e.g., dietary), or phylogenetic patterns is unknown. It would be interesting to extend long bone material and histological analyses to the other cercopithecoid taxa included in the present study, which encompass a wider range of behavioral variation as well as a wider sampling of different phylogenetic lineages (Table 1).

Articular surface parameters Surface areas of the femoral and humeral heads were only approximated here, using linear measurements and geometric formulae based on idealized partial spheres (Ruff, 2002), which undoubtedly introduced some error. However, very high correlations and relatively low %SEE have been reported when predicting surface areas or volumes of these articulations determined more directly using latex molds with those calculated from linear measurements (Godfrey et al., 1995; Rafferty, 1996; Ruff, 2002), and these results were replicated here for humeral head surface area in four of the taxa included in the present study. Thus, the linear measurement and geometric modeling technique appears to give accurate and unbiased results when compared to more direct assessment of surface areas. Use of the geometric modeling technique also allowed inclusion of data collected earlier for another study (Ruff, 2002), as well as many more specimens from the Taï study samples. In addition, these results suggest that future articular data (and calculated intra- and inter-limb indices) collected using more direct methods should be comparable to those of the present study.

Of course, in addition to overall surface area and size (i.e., breadth), other aspects of articular morphology, orientation, and positioning relative to adjacent structures also influence degree of mobility in different anatomical planes (Jenkins and Camazine, 1977; Gebo et al., 1988; Harrison, 1989; Rose, 1989; Larson, 1993; MacLatchy and Bossert, 1996; Dunham et al., 2015). The fact that a moderate to strong (with adjustment of Asian langur climbing values) correlation between relative surface area of the humeral head and climbing frequency is still apparent within the present study samples suggests that the simpler measures employed here are capturing some of the more functionally salient aspects of articular form, however. Within-bone pairing of articular parameters with diaphyseal strengths probably also increased the specificity of the functional signals, i.e., in terms of joint excursion relative to overall limb loading (Ruff, 2002).

Behavioral categories There are many issues to be considered when attempting to combine behavioral data collected by different observers using different methodologies (Dagosto and Gebo, 1998). Although reported statistics were transformed here when necessary to create as nearly comparable representations of behavior as possible (e.g., converting from percentage of total observations to percentage of total movement, adjusting for different definitions of 'climbing'), there are still many uncertainties in the resulting data. Among the taxa included in the present study, a variety of methods were used to record locomotor behavior and calculate frequencies, including percent of bouts observed via point sampling (Caldecott, 1986; McGraw, 1998, 2000), percent of bouts observed via continuous sampling (Fleagle, 1978; Gebo and Chapman, 1995), percent of time observed via continuous sampling (Rose, 1977), and percent of distance traveled via continuous sampling (Cant, 1988). Different age/sex classes were included in different studies (see above for details). In some cases, variable habituation may have influenced results. Length of observation varied greatly between studies, potentially producing seasonal biases. Behavioral data were not always matched with the same locations that skeletal data were collected from, and in some cases (*Papio*, *Trachypithecus*, *Presbytis*) closely related species were used to derive behavioral data, although care was taken to match both taxa and environments as far as possible. Problems with variable definitions of 'climbing' were discussed earlier (also see Rose, 1979; Fleagle et al., 1981; Gebo and Chapman, 1995; Hunt et al., 1996; Moffett, 2000 for further discussion). In one case (Fleagle, 1978) no compensation for a different definition that included more horizontal travel could be made; the effects of this on the present study results were probably significant, as shown above. In another case (Caldecott, 1986), the description of this locomotor category was so non-specific (and results were so incongruous with other reported observations for the species) that climbing data were not included in the present study. 'Leaping' appeared to be more consistently defined between investigators, but even here there was some variation; for example, Rose (1977:20) noted that among the baboons in his study, "no long distance jumps were observed and the hind limb thrust at take-off was never great", which contrasts with the leaping behaviors described for most other taxa in the study. Leaping and horizontal 'bounding' share some kinematic and likely substrate reaction force similarities (Morbeck, 1976), but the latter is included within quadrupedal running in the behavioral studies utilized here, where it is distinguished at all (in *C. polykomos*).

Another important consideration in interpreting behavioral data is the actual amount of time spent by individuals engaging in the specified activity. Here, as in most studies that attempt to relate behavior and postcranial skeletal morphology (e.g., Fleagle, 1976b;

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[3] It is also possible that artifacts associated with the pQCT scanner itself may have influenced bone mineral density results. Partial volume artifacts have been shown to occur when measuring mineral density in cortical bone phantoms of varying wall thicknesses, using a different pQCT scanner (Augat et al., 1998). However, scanner resolution was much coarser in that study, with a pixel size of 0.59 mm and scan thickness of 2.5 mm, compared to a pixel size of 0.15 mm and scan thickness of 1.0 mm used in the present study. Also, if partial volume artifacts were significant, mineral densities would be expected to decrease in smaller specimens (i.e., the cercopithecoids in the present study), given their larger predicted artifacts, relative to larger specimens (e.g., humans and gorillas), while we found the opposite to be true. Therefore, methodological issues associated with the scanning itself are unlikely to explain our results.

Fleagle and Meldrum, 1988; Gebo and Sargis, 1994), percentages of total locomotor behavior were used to evaluate climbing and leaping behavior. However, depending on the overall activity budget of the individual or taxon, this may present misleading information on the amount of time spent in that particular behavior relative to other taxa. For example, the baboons in Rose's (1977) study spent about 75% of the day sitting, standing, or lying down; thus, actual frequencies of leaping or climbing relative to the total observation period were lower than those used here, as discussed above. Locomotor behavior as a percentage of total positional behavior is even smaller in many primate taxa: in another study, Rose (1979) noted that locomotor behavior accounted for only 4.5% of observed time in vervets, and 1.1% of observed time in black-and-white colobus (*C. guereza*). Morbeck (1977) made the same observation regarding the latter species. The effects of such differences are apparent when one makes comparisons across species. In Rose's (1979) study, although *C. guereza* leapt about twice as often as vervets as a percentage of locomotion, because of the higher overall activity rate of vervets, they actually leapt about twice as often per hour than *C. guereza*. In one sense, expressing behaviors such as leaping and climbing as a percentage of total locomotor behavior may be justifiable, since locomotor behavior would be expected to create higher mechanical demands on the musculoskeletal system (i.e., higher joint reaction forces, higher bending and torsional loads on diaphyses) than positional behavior. Thus, if musculoskeletal adaptations are viewed as the product of competing demands of different components of the total locomotor repertoire (e.g., leaping, climbing, quadrupedal walking and running, suspension), then percentage of locomotor behavior as a comparative metric may be reasonable. It should also be recognized that "the time spent on a specific locomotion is not necessarily connected with the magnitude of its influence on the musculo-skeletal design of a species" (Isler, 2005:67). For example, being able to climb large-diameter supports efficiently and safely may be a fairly rarely employed, but still ecologically significant activity for some taxa.

This is not to say that positional behavior, such as forelimb reaching movements involved in foraging (Dunham et al., 2015, 2017), cannot also be important influences on limb bone morphology. 'Climbing' in the broader sense that includes quadrumanous scrambling, clambering, and movements among irregular supports, has been defined in part on the basis of variability in limb orientation (Gebo and Chapman, 1995), which is also evinced in positional behaviors (Cant, 1987; Dunham et al., 2015). Climbing was limited here (as far as possible) to vertical movements in part to distinguish it from more generalized movement capabilities. However, there is still overlap between locomotor and positional requirements, e.g., abduction and elevation of the forelimb in either vertical reaching (while stationary) or climbing. Unusual joint surface (and limb length) proportions apparently not related to locomotor behavior but possibly attributable to forelimb positional behavior have been noted in *Theropithecus oswaldi* (Jolly, 1972; Krentz, 1993; Ruff, 2002). The greater phylogenetic signal and probable higher degree of genetic canalization characteristic of external articular morphology relative to diaphyseal cross-sectional properties (see above) may also play a role in creating such morphological 'mosaics' (Ruff et al., 2018a).

5. Conclusions

In many respects, results of the present study of femoral and humeral structural proportions in 13 cercopithecid species parallel those found in comparisons among catarrhines more generally (Ruff, 2002). More frequently leaping species have relatively stronger femoral diaphyses, and this is true even when bone length differences are factored in. This can be attributed to the very large

peak substrate reaction forces on the hind limb during take-off in leaping. More frequent leapers also have relatively larger femoral compared to humeral articulations, due to predicted higher hind limb joint reaction forces. This is more evident for general joint size (breadth) proportions than for surface areas, however, likely because surface areas are more directly related to joint excursion, which does not (necessarily) covary with leaping frequency. Humeral head articular surface area relative to diaphyseal strength is larger in more frequent climbers. This can be attributed to the need for more varied forelimb positions during vertical climbing, in particular shoulder abduction and elevation.

However, contrary to patterns among catarrhines as a whole, including hominoids (Ruff, 2002), femoral head surface area or breadth relative to diaphyseal strength is not greater in more frequent cercopithecid climbers. This may be attributable to different climbing styles in cercopithecoids versus hominoids, with cercopithecoids employing less foot inversion and hip abduction, which would not favor larger hind limb joint surface areas. This is also consistent with relatively more conservative foot structure across cercopithecoids, and is possibly related to a terrestrial or semiterrestrial origin for the clade (Strasser, 1988; Gebo, 1989, 1993; Meldrum, 1989; Benefit, 1999). Because of the different trends in fore- and hind limb articulations, more frequent cercopithecid climbers have relatively large humeral compared to femoral heads. Unlike comparisons including hominoids, femoral/humeral diaphyseal strength proportions are not associated with climbing frequency, which again is consistent with a different climbing style in cercopithecoids that does not involve an increase in forelimb loading relative to other forms of quadrupedal locomotion.

Relationships between locomotor behavior and skeletal structure are strongly influenced by phylogeny for all proportions involving articulations, but this is not the case for shaft strength proportions, which may reflect the greater developmental plasticity of long bone diaphyseal cortices in response to mechanical loadings. In any event, functional relationships between behavior and morphology are apparent even when controlling for phylogeny, for both diaphyses and articulations. This suggests that these characteristics may also be useful in reconstructing locomotor behavior in fossil taxa, on both narrower (i.e., cercopithecid) and broader (catarrhine or anthropoid) taxonomic scales.

Supplementary Online Material

Supplementary online material to this article can be found on-line at https://doi.org/10.1016/j.jhevol.2019.04.003.

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