

Comparative Postcranial Body Shape and Locomotion in *Chlorocebus aethiops* and *Cercopithecus mitis*

F. Anapol,^{1*} T.R. Turner,¹ C.S. Mott,¹ and C.J. Jolly²

¹Department of Anthropology, University of Wisconsin-Milwaukee, Milwaukee, Wisconsin 53201

²Department of Anthropology, New York University, New York, New York 10003

KEY WORDS cercopithecine; limb proportions; sexual dimorphism; locomotion; social organization

ABSTRACT Body weight and length, chest girth, and seven postcranial limb segment lengths are compared between two guenon species, *Chlorocebus* (*Cercopithecus*) *aethiops* (vervets) and *Cercopithecus mitis* (blue monkeys), exhibiting different habitual locomotor preferences. The subjects, all adults, were wild caught for a non-related research project (Turner et al. [1986] Genetic and morphological studies on two species of Kenyan monkeys, *C. aethiops* and *C. mitis*. In: Else JG, Lee PC, editors. Primate evolution, proceedings of the Xth International Congress of Primatology, Cambridge. London). The morphological results are interpreted within the context of previously published observations of primate locomotion and social organization. The sample is unique in that the body weight of each individual is known, allowing the effects of body-size scaling to be assessed in interspecific and intersexual comparisons. *C. mitis* has a significantly ($P < 0.05$) greater body weight and trunk length than *C. aethiops*. A shorter trunk may function to reduce spinal flexibility for ground-running in the latter. Proximal limb segments (arm and thigh) are significantly greater in *C. mitis*, reflecting known adaptations to committed arboreal quadrupedal locomotion.

Primate postcranial morphology is inextricably linked to locomotion, although not to the exclusion of the influences of substrate habitation and social organization. The extent to which a contributing behavioral variable affects even the most fundamental morphological characteristics, e.g., relative limb proportions and sexual size dimorphism, remains unclear, even when morphological interpretation focuses on a specific locomotor preference. This is because limb proportions reflect both the effects of scale due to body size and preferred locomotor modality (e.g., Fleagle, 1985; Jungers, 1985, 1988). Limb proportions are determined by both locomotor morphology and sexual size dimorphism (Clutton-Brock and Harvey, 1977). Both are influenced by how narrow or broad a species' habitat might be, e.g., strictly arboreal or terrestrial, by contrast to dividing its time and/or behavioral activities (e.g., feeding, traveling, or resting) between canopy and ground. Social organization, and its effect on sexual size dimorphism (e.g., Kay et al., 1988; Plavcan et al., 1995; Plavcan and van Schaik, 1997), can also

pedal locomotion. By contrast, relative distal limb segments (forearm, crus, and foot) are significantly longer in *C. aethiops*, concordant with a locomotor repertoire that includes substantial terrestrial quadrupedalism, in addition to arboreal agility, and also the requisite transition between ground and canopy. Although normally associated with arboreal monkeys, greater relative tail length occurs in the more terrestrial vervets. However, because vervets exploit both arboreal and terrestrial habitats, a longer tail may compensate for diminished balance during arboreal quadrupedalism resulting from the greater "brachial" and "crural" indices that enhance their ground quadrupedalism. Most interspecific differences in body proportions are explicable by differences in locomotor modalities. Some results, however, contradict commonly held "tenets" that relate body size and morphology exclusively to locomotion. Generally associated with terrestriality, sexual dimorphism (male/female) is greater in the more arboreal blue monkeys. A more intense, seasonal mating competition may account for this incongruity. Am J Phys Anthropol 127:231–239, 2005.

© 2004 Wiley-Liss, Inc.

hinder the interpretation of size and limb proportions within the context of locomotion.

For better or worse, when considered individually, behavioral variables each tend to be associated with a widely held generalization about primate morphology. For example, arboreal quadrupedal monkeys generally have shorter distal fore- and hindlimb segments, and longer tails, by contrast to their terrestrial relatives (Hildebrand, 1974; Rodman, 1979;

Grant sponsor: National Science Foundation; Grant numbers: BNS77-03322, DBS-9221795, BNS81-04435.

*Correspondence to: Fred Anapol, Department of Anthropology, University of Wisconsin-Milwaukee, P.O. Box 413, Sabin Hall, Milwaukee, WI 53201. E-mail: fred@uwm.edu

Received 8 July 2003; accepted 17 February 2004.

DOI 10.1002/ajpa.20055
Published online 22 October 2004 in Wiley InterScience (www.interscience.wiley.com).

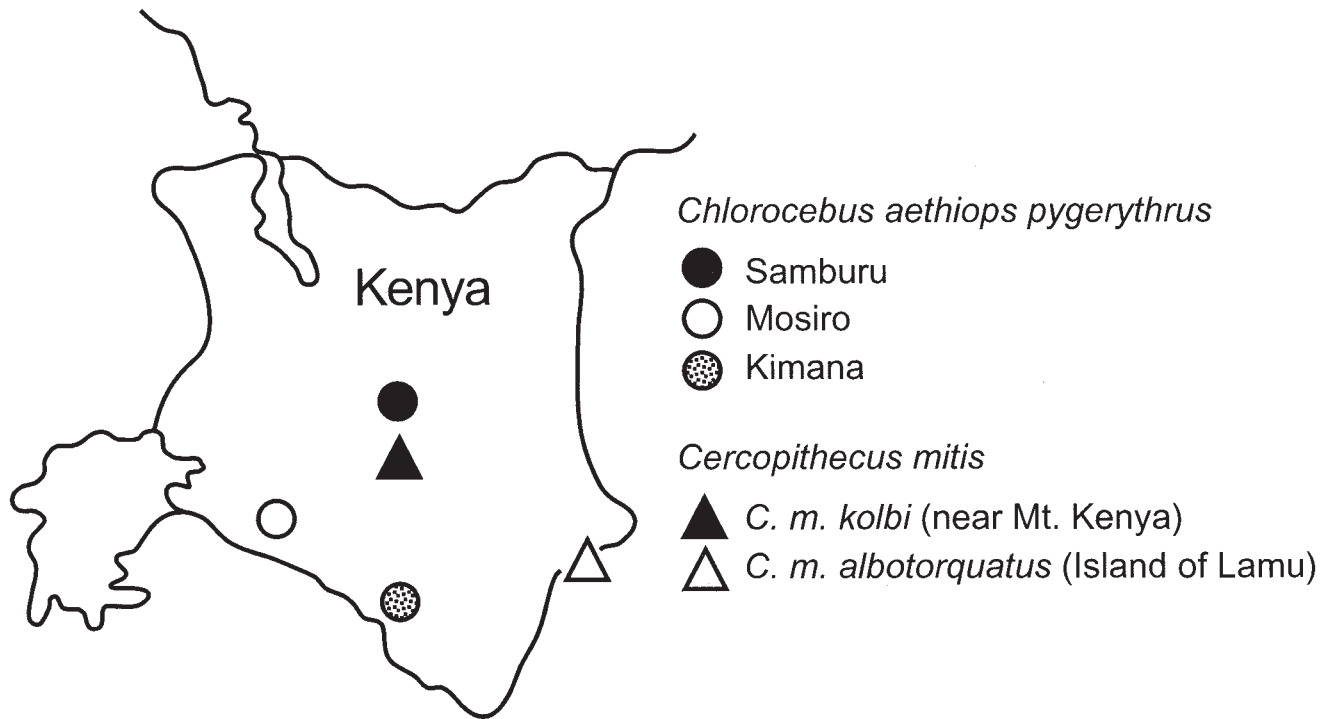


Fig. 1. Approximate geographical location of sites from which data used in this study were collected (adapted from Turner et al., 1986).

Rollinson and Martin, 1981; Fleagle, 1999; Gebo and Sargis, 1994). Sexual size dimorphism is thought to be greater in terrestrial than in arboreal species (Clutton-Brock and Harvey, 1977) due to ecological agents, e.g., energetic limitations (Jorde and Spuhler, 1974). Larger male-body size:female-body size ratios also are predicted for species in which males are highly competitive for females (Kay et al., 1988).

In this investigation of body and postcranial size, we compare relative body size and lengths of limb segments between two quadrupedal guenon species that occupy somewhat different substrates: the semiterrestrial *Chlorocebus aethiops* and the more committed arborealist, *Cercopithecus mitis* (Kingdon, 1974; Rose, 1979; Gebo and Sargis, 1994; Gebo and Chapman, 1995). Our objectives are to 1) identify interspecific differences and sexual dimorphism in body segment lengths, and 2) interpret differences with respect to habitual substrate occupation and social behavior. Because the body weights of the individuals (all wild-caught) used in this study are known, the effects of body-size scaling on comparisons can be controlled.

MATERIALS AND METHODS

The sample for this study consists of 109 vervets (*Chlorocebus aethiops pygerythrus*) and 69 blue monkeys (25 *Cercopithecus mitis albotorquatus* and 54 *C. m. kolbi*). The vervets were trapped at three sites in south and central Kenya (Fig. 1), and represent 21 troops at locations separated by 80–300 km. These sites differ in altitude, temperature, and

mean annual rainfall, resulting in significant intersite size differences for adult females but not adult males (Turner et al., 1997).¹ The blue monkeys were from two separate Kenyan sites (Fig. 1): *C. m. albotorquatus* from the island of Lamu at sea level off the southeast (Indian Ocean) coast, and *C. m. kolbi* from central Kenya. All animals were living and had been sedated for a previously published genetic study (Turner et al., 1986).

For each individual, body weight was recorded to the nearest 0.01 kg. The following linear variables were measured with cloth tape and reported to the nearest 0.01 cm (Fig. 2): body length (B), external occipital protuberance to base of tail; chest girth (G), circumference of widest part of the chest under the

¹Intersite differences in female body weight and segment measurements for vervets are published in Turner et al. (1997). In that paper, we concluded that the body weights of the monkeys studied at Naivasha were inflated due to their having better access to human foods. Consequently, the data from the Naivasha monkeys are not included in the current study. Similar intersite differences may also occur in blue monkeys. A potential effect on the current study is that, in females, standard deviations may be slightly greater than site-specific values. The bearing on the results presented here is the possible absence of significant ($P < 0.05$), yet biological, between-sex differences in the standardized segment measurements for a few of the variables. Accordingly, our interpretations in Results, Discussion, and Conclusions focus on interspecific and not intersexual comparisons, and are largely unaffected by the latter. Furthermore, since the primary focus of this study is to relate interspecific differences in limb segment lengths to interspecific differences in locomotor behavior, none of the latter having been field-collected for this study, pooling data from all sites seems more appropriate.

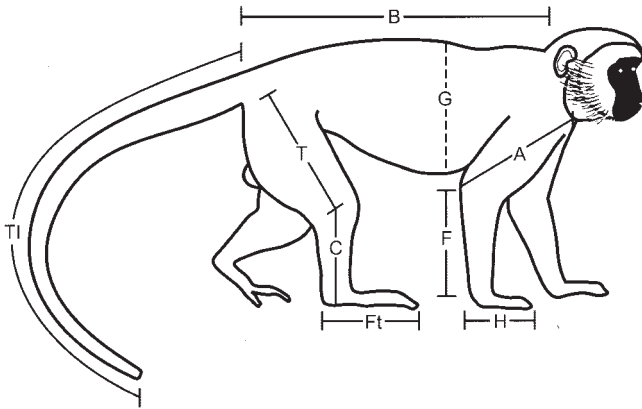


Fig. 2. Labels indicate endpoints of measurements taken on subjects with limb and tail joints fully extended. B, body length; G, chest girth; A, arm length; F, forearm length; H, hand length; T, thigh length; C, crus length; Ft, foot length; TI, tail length. See Materials and Methods for description of endpoints.

forelimb (Schultz, 1929) during shallow breathing; arm length (A), tip of the acromion process to tip of the olecranon process with elbow fully extended; forearm length (F), tip of the olecranon process to flexion crease at the carpus; hand length (H), flexion crease at the carpus to tip of the middle manual digit; thigh length (T), highest point of the greater trochanter to midpoint of the disto-lateral margin of the lateral condyle of the femur; crus length (C), midpoint of the disto-lateral margin of the lateral condyle of the femur to tip of the heel in dorsiflexion; foot length (Ft), tip of the heel to tip of the longest pedal digit; and tail length (TI), base to tip of the tail. Measurements of vervets were made under supervision of T.R.T. Measurements of all blue monkeys were made by C.S.M., after extensive training by T.R.T.

Each body and limb segment was normalized by dividing its length by the cube root of body weight (Sneath and Sokal, 1973). This approach eliminates most of the variance due simply to body size differences while preserving size-related shape information, and is statistically equivalent to Mosimann's approach using logged ratios (Mosimann, 1970; Jungers, 1988; Falsetti et al., 1993; Jungers et al., 1995).

For comparison with previous studies, several indices ordinarily determined from direct bone measurements and commonly used in the comparative analysis of locomotor modalities were calculated from the measured variables *before* normalization to body size: "intermembral" index, $100 \times (\text{arm} + \text{forearm}) / (\text{thigh} + \text{crus})$; "humerofemoral" index, $100 \times \text{arm} / \text{thigh}$; "brachial" index, $100 \times \text{forearm} / \text{arm}$; "crural" index, $100 \times \text{crus} / \text{thigh}$; and tail-length: body-length ratio. Because these indices were computed from measurements of limb segments rather than bones, comparisons with previously published indices based on measurements of bones were accomplished by restricting the language to rank order of dyads, e.g., "relatively larger (smaller)."

Thus, the normalized variables are compared to an a priori size prediction with males and females treated separately, thereby largely eliminating the bias present in empirically derived equations (Smith, 1984). Means of normalized variables and indices were tested for significant differences between sexes and between species using Student's *t*-test (Sokal and Rohlf, 1981).

To facilitate interpretation of some results, the overall relationship between sexual size dimorphism and body size was assessed by subjecting previously published (Fleagle, 1999, citing others) mean male and female body weights of 163 primate species, including 50 cercopithecine species, to statistics of association (Pearson's moment correlation and linear regression) (Sokal and Rohlf, 1981). Male body weight/female body weight was regressed on (and correlated with) female body weight following Smith (1999, after Lovich and Gibbons, 1992). All computations and statistical analyses were accomplished using the Statistical Analysis System (SAS Institute, Cary, NC) on the IBM mainframe computer (UWM-3270) at the University of Wisconsin-Milwaukee.

RESULTS

Means and standard deviations of raw and calculated (indices) variables are presented in Table 1, separated by species and sex.

Significant ($P < 0.05$) differences between size-adjusted means are indicated in Table 2 for comparisons between sexes for each species, and between species for females (only), males (only), and both sexes pooled.

Cercopithecus mitis is significantly larger (either sex, $P < 0.05$) and more sexually dimorphic (mean male:mean female ratio, ~ 1.87) than *Chlorocebus aethiops* (~ 1.54), with sexual size dimorphism (SSD) significant ($P < 0.05$) within both species (Table 1). No size-adjusted sexual dimorphism occurs in either species for body length, chest girth, forearm length, thigh length, tail length, forelimb (upper arm plus forearm) length, or humerofemoral, crural, or tail: body length indices (Table 2). In vervets, relative hand length, crus length, and hindlimb length are greater in males, while the intermembral index is greater in females. In blue monkeys, males have relatively longer arms, while females have relatively longer feet and a greater brachial index.

Interspecific differences are significant ($P < 0.05$) for females, males, and both sexes pooled, and are entirely lacking only for chest girth and forelimb length (Table 2). In addition to body weight, blue monkeys are relatively larger than vervets in body length, arm length, thigh length, hindlimb length (not males), and humerofemoral index (males only). Vervets are relatively larger than blue monkeys in forearm length, hand length (males only), crus length (not females), foot length, tail length, and intermembral (females only), brachial, crural, and tail:body length indices. Because total hindlimb

TABLE 1. Means (+ standard deviation) of raw variables and calculated indices

	Chlorocebus aethiops				Cercopithecus mitis			
	Females		Males		Females		Males	
	n	Mean (S.D.)	n	Mean (S.D.)	n	Mean (S.D.)	n	Mean (S.D.)
Body weight (kg)	61	2.74 (0.38)	48	4.21 (0.58)	34	4.25 (1.01)	33	7.93 (1.90)
Body length (cm)	61	35.78 (2.46)	48	41.04 (2.84)	33	42.98 (3.78)	34	51.84 (5.90)
Chest girth (cm)	54	28.35 (1.82)	44	32.80 (2.34)	35	32.80 (4.08)	34	40.86 (4.96)
Arm length (cm)	61	12.34 (1.15)	48	14.32 (1.05)	35	15.35 (1.20)	34	19.72 (2.09)
Forearm length (cm)	61	12.62 (0.64)	48	14.70 (1.09)	35	13.47 (1.60)	34	16.31 (1.53)
Hand length (cm)	61	7.99 (0.70)	47	9.50 (0.60)	35	9.27 (1.06)	33	11.15 (1.29)
Thigh length (cm)	61	13.70 (0.86)	48	16.18 (0.99)	35	17.18 (1.80)	34	21.15 (1.87)
Crus length (cm)	61	13.83 (0.87)	48	16.42 (0.91)	35	15.65 (1.27)	34	19.47 (1.70)
Foot length (cm)	60	12.06 (0.63)	48	14.03 (0.83)	35	13.49 (1.14)	34	15.95 (1.69)
Tail length (cm)	61	54.86 (4.03)	47	64.56 (4.81)	30	54.68 (7.10)	33	68.24 (1.29)
Forelimb length (cm)	61	24.97 (1.55)	48	29.02 (1.92)	35	28.82 (2.25)	34	36.03 (3.12)
Hindlimb length (cm)	61	27.53 (1.54)	48	32.60 (1.74)	35	32.83 (2.69)	34	40.62 (3.36)
"Intermembral" index	61	91 (4)	48	89 (4)	35	88 (7)	34	89 (8)
"Humerofemoral" index	61	90 (6)	48	89 (6)	35	90 (9)	34	94 (10)
"Brachial" index	61	103 (8)	48	103 (7)	35	89 (10)	34	83 (9)
"Crural" index	61	101 (6)	48	102 (5)	35	92 (8)	34	92 (5)
Tail: body length ratio	61	1.5 (0.2)	47	1.6 (0.2)	28	1.3 (0.1)	33	1.3 (0.1)

TABLE 2. Table of significant ($p < 0.05$) intersexual and interspecific differences between means of measured variables (size-adjusted) and calculated indices¹

	Intersexual		Interspecific		
	V	M	♀	♂	♀ + ♂
Body weight	♂	♂	M	M	M
Body length			M	M	M
Chest girth					
Arm length		♂	M	M	M
Forearm length			V	V	V
Hand length	♂			V	
Thigh length			M	M	M
Crus length	♂			V	V
Foot length		♀	V	V	V
Tail length			V	V	V
Forelimb length					
Hindlimb length	♂		M		M
"Intermembral" index	♀		V		
"Humerofemoral" index				M	
"Brachial" index		♀	V	V	V
"Crural" index			V	V	V
Tail: body length			V	V	V

¹ Symbols appear when differences are significant and indicate which group had larger mean value V, vervets; M, *mitis*; ♀, females; ♂, males.

length (thigh plus crus) is significantly greater in *C. mitis*, both in females and with both sexes pooled, the "intermembral" index is below 100 for both species, although significantly different ($P < 0.05$) only for females.

Results from computations on previously published (Fleagle, 1999, citing others) body weights (male/female regressed on and correlated with male and female body weights separately) are shown in Table 3. For context, results are shown for the entire sample, and separately for hominoid (excluding humans), cercopithecine, colobine, cebid, and callitrichid primates. Of all groups, cercopithecines have the highest SSD at 1.62, with male and female body weights highly correlated ($P < 0.0001$). In cercopithecines, SSD is significantly correlated with both female and male body weight. The slopes for both regressions are near isometry (0.02). Female body

weight accounts for 0.11 (r^2) of the variation, while male body weight accounts for 0.29 (r^2) of the variation.

DISCUSSION

The interspecific differences in relative body size and limb proportions presented here demonstrate contrasting morphological adaptations to differences in locomotor preferences. Ironically, both species exhibit similar relative percentages of quadrupedalism, leaping, and climbing (Rose, 1979; Gebo and Chapman, 1995). Nevertheless, interspecific differences in relative limb segment lengths and related indices associate consistently and predictably to contrast committed arboreal quadrupedalism, as practiced by *Cercopithecus mitis*, and a similar locomotor repertoire that also includes substantial terrestrial quadrupedalism, in addition to arboreal agility, as was documented for *Chlorocebus aethiops* (Rose, 1979; Gebo and Chapman, 1995; McGraw, 1996). By contrast, differences in male:female body weight ratios reported here for blue monkeys and vervets contradict a commonly held perception that terrestrial primates are more sexually dimorphic than arboreal primates (see Clutton-Brock and Harvey, 1977). This may be more clearly understood with consideration of interspecific differences in social organization (see below).

Comparative locomotor morphology

Most of the published literature on comparative body proportions and their association with documented studies of wild animal locomotion consists of measurements of disarticulated bones from museum specimens. All measurements in this study, however, were taken directly from anesthetized living animals and likely provide somewhat different, yet proportionally accurate, values than those taken directly on bones. Therefore, to facilitate placement of the current results within the context of prior work, comparisons are interpreted in terms of published

TABLE 3. Results from correlation and regression analyses on body weight data compiled in Fleagle (1999)¹

	n	r: M vs. F		Mean: SSD	
All	164	0.96 (0.0001)		1.32 (0.35)	
Hominoidea ²	18	0.95 (0.0001)		1.40 (0.53)	
Cercopithecinae	50	0.96 (0.0001)		1.62 (0.24)	
Colobinae	28	0.86 (0.0001)		1.24 (0.25)	
Cebidae	42	0.96 (0.0001)		1.17 (0.20)	
Callithrichidae	26	0.95 (0.0001)		0.99 (0.08)	
M/F regressed on F		r	Slope	Int	r ²
All	164	0.43 (0.0001)	0.01 (0.00)	1.23 (0.03)	0.18
Hominoidea ²	18	0.71 (0.00)	0.01 (0.00)	1.01 (0.13)	0.51
Cercopithecinae	50	0.32 (0.02)	0.02 (0.01)	1.48 (0.07)	0.11
Colobinae	28	0.47 (0.01)	0.06 (0.02)	0.76 (0.18)	0.23
Cebidae	42	0.17 (0.29)	0.01 (0.01)	1.13 (0.05)	0.03
Callithrichidae	26	0.23 (0.26)	0.17 (0.15)	0.91 (0.07)	0.05
M/F regressed on M		r	Slope	Int	r ²
All	164	0.52 (0.0001)	0.01 (0.00)	1.23 (0.03)	0.27
Hominoidea ¹	18	0.87 (0.00)	0.01 (0.00)	1.01 (0.09)	0.75
Cercopithecinae	50	0.53 (0.0001)	0.02 (0.00)	1.43 (0.05)	0.29
Colobinae	28	0.85 (0.0001)	0.06 (0.01)	0.70 (0.07)	0.72
Cebidae	42	0.39 (0.01)	0.02 (0.01)	1.08 (0.04)	0.15
Callithrichidae	26	0.50 (0.01)	0.35 (0.12)	0.84 (0.05)	0.25

¹r, Pearson's product-moment correlation coefficient (probability that r = 0); M, males; F, females; SSD, sexual size dimorphism; Int, y-intercept (standard error); r², coefficient of variation; standard error for slope also is shown. ² Excluding humans.

TABLE 4. Some comparative results from previous studies (discussed in text)¹

Species	Fleagle, 1977		Rodman, 1979		Fleagle and Meldrum, 1988		Gebo and Sargis, 1994		
	<i>Trachypithecus obscura</i>	<i>Presbytis melalophos</i>	<i>Macaca fascicularis</i>	<i>Macaca nemestrina</i>	<i>Chiropotes satanas</i>	<i>Pithecia pithecia</i>	<i>Chlorocebus aethiops</i>	<i>Cercopithecus mitis</i>	<i>Erythrocebus patas</i>
Habitat	Arboreal	Arboreal, with leaping and forelimb suspension	Arboreal	Semiterrestrial	Arboreal	Arboreal, with leaping and clinging	Terrestrial	Arboreal	Terrestrial
Weight (kg), F/M ²	6.3/7.9	6.5/6.6	3.6/5.4	6.5/11.2	2.6/2.9	1.6/1.9	3.0/4.3	4.3/7.9	5.8/10.6
Indices									
Intermembral	85	78	93	94	83	76	83	80	93
Brachial	98	114	98	100	86	92	97	96	106
Crural	89 ³	92 ³	95	93	87	92	93	97	97
Humerofemoral			92	90	82	76	81	80	91
Tail			Long	Short					
Foot length (cm)	15.4	16.3							

¹ Preferred mode of locomotion indicated by author(s) is indicated, with additional significant locomotor components noted in some cases. ² From Fleagle, 1999. ³ Calculated from Strasser, 1992.

comparative dyads (Table 4), i.e., relative results from vervets and blue monkeys are compared to relative results from *Trachypithecus obscura* and *Presbytis melalophos* (Fleagle, 1977), *Macaca fascicularis* and *M. nemestrina* (Rodman, 1979), *Chiropotes satanas* and *Pithecia pithecia* (Fleagle and Meldrum, 1988), and *Chlorocebus aethiops*, *Cercopithecus mitis*, and *Erythrocebus patas* (Gebo and Sargis, 1994), all of which are from measurements of disarticulated bones.

Body size. That vervets spend a considerable amount of time on the ground is well-documented (Kingdon, 1974; Rose, 1979; Gebo and Chapman, 1995). Vervets are relatively small, both for their brain size (Manaster, 1979), and among other generally ground-dwelling cercopithecines, e.g., baboons. Nevertheless, it is somewhat surprising that their body weight is so much less than that of *C. mitis*. However, because they are smaller relative to

the substrate then *mitis*, vervets may be able to progress along large boughs in a manner more similar to that by which they walk and run on the ground, i.e., using more terrestrial-like adaptations while retaining substrate versatility (Manaster, 1979). A comparable phenomenon was suggested by Jenkins (1974) for tree shrews.

Body length. Among catarrhine primates, skeletal trunk length scales negatively allometric with body weight (Majoral et al., 1997). Thus, *C. mitis*, having a body weight almost twice that of vervets, would expectedly have a considerably shorter relative trunk length. The results presented here, however, show that relative trunk length is significantly ($P < 0.05$) shorter in *vervets* than in blue monkeys.

Comparing vervets with patas monkeys, Hurov (1987) described differences in locomotor anatomy and terrestrial locomotion that can be incorporated

into a trajectory that includes the current comparison of blue monkeys and vervets. Vervets have greater flexibility in their spine than do the more terrestrial patas monkeys, attributable to thicker intervertebral discs (Hurov, 1987), but likely less flexibility than blue monkeys.

Body length seems better correlated than body weight to the degree of terrestriality practiced by a species. Vertebral column function in ground-running primates is described as more closely resembling that of the dorsistable ungulate cursors than of the dorsimobile carnivores (Gambarayan, 1974; Vangor, 1979; Hurov, 1987). Clearly, terrestrial Old World monkeys do not run like nonprimates, since, having been derived from early arboreal precursors, as are all primates, they need to retain prehensile function in their anterior cheir (Larson, 1998). However, like the ungulates, terrestrial monkeys are "all arms and legs" while running, and a shortened back may reduce instability between fore- and hindquarters.

Limb and limb segment indices. Based on previously published results, McGraw (2002) concluded that, among guenons, the percentage of a species' locomotory repertoire occupied by leaping is inversely correlated to its intermembral index. In the current study, intermembral index does not distinguish vervets from blue monkeys. This is consistent with comparable results from measurements taken on disarticulated bones (Table 4) which did not distinguish between these same species (Gebo and Sargis, 1994) or between species of another arboreal/terrestrial quadrupedal dyad, *Macaca fascicularis* and *M. nemestrina* (Rodman, 1979). By contrast to these latter species, neither of which practices leaping as part of its locomotor repertoire (Rodman, 1979), when an arboreal quadruped that *does not* include leaping in its locomotor repertoire is compared to one that *does*, e.g., *Trachypithecus obscura* vs. *Presbytis melalophos* (Fleagle, 1977) or *Chiroptotes satanas* vs. *Pithecia pithecia* (Fleagle and Meldrum, 1988), the "leaper" has a considerably lower intermembral index. Gebo and Sargis (1994) found the intermembral index in the terrestrial *Erythrocebus patas* to be similar to what Rodman (1979) reported for both macaque species but considerably higher than what they found for vervets and blue monkeys. The results in the current study for vervets and blue monkeys are only slightly lower than those reported by Rodman (1979) for macaques.

The humerofemoral index is somewhat greater in blue monkeys than in vervets. This parallels the *fascicularis/nemestrina* dyad in which the arboreal *fascicularis* has a slightly higher humerofemoral index than the semiterrestrial *nemestrina* (Rodman, 1979). A relatively longer humerus, vis-à-vis the femur, may be required by an arboreal quadruped to provide longer attachment sites for shoulder muscles (Anapol and Gray, 2003) and/or better leverage

for ascent and descent in the canopy, and to modulate its horizontal attitude during descent.

Terrestrial running and galloping in primates are also strongly associated with intralimb proportions. Higher distal segment:proximal segment ratios, i.e., brachial and crural indices, are generally found in the more cursorial terrestrial species (Hildebrand, 1974), and expectedly, both indices are considerably higher in the more terrestrial *C. aethiops* than in *C. mitis*. Because both species are fundamentally arboreal, the interspecific differences in the relative proportions of proximal and distal limb segments likely reflect an adaptation for the rapid terrestrial quadrupedalism of vervets. Having longer distal limb segments, however, may somewhat compromise balance for *C. aethiops* when in the trees (see below).

Although our results for brachial and crural indices conform to expectations about the differences between arboreal and semiterrestrial species, expectations based on previous studies of arboreal, semiterrestrial, and terrestrial species (e.g., Rodman, 1979; Gebo and Sargis, 1994) exhibit some contradictions (Table 4). For example, the more terrestrial *M. nemestrina* has only slightly *higher* brachial yet slightly *lower* crural indices² than those of the more arboreal *Macaca fascicularis* (Rodman, 1979). Gebo and Sargis (1994) found a significantly higher crural index in the arboreal *C. mitis* than in *C. aethiops* (which they classified as "terrestrial" rather than "semiterrestrial"), although no significant difference occurs in the brachial index. As expected, the brachial index of both vervets and *mitis* is lower than in patas monkeys (Gebo and Sargis, 1994). The crural index, however, of the primarily terrestrial patas monkey is midway within the 10-point spread calculated in the current study, and separates the semiterrestrial vervet (larger value) from the arboreal *mitis*. This may imply that the larger crural index in vervets may be related to the transition from ground to canopy, thus supporting the concept of semiterrestriality as a unique locomotor modality, rather than as a reflection of an "animal's mode-shifting" between trees and ground (see Evolutionary Implications, below). None of these indices appear to be correlated to body size, i.e., in some of these paired comparisons the larger species has either higher or lower values for one or another index. This argues against the notion that index differences are totally the result of simple size differences or a uniform pattern of growth allometry.

Other comparable available data (Table 4) include dyads of langurs (Fleagle, 1977) and pithicine cebids (Fleagle and Meldrum, 1988). Both of these studies compared closely related arboreal quadrupeds, with one of each pair exhibiting a higher proportion of leaping and clinging and/or climbing behavior that can be correlated to differences in their

²Rodman (1979) presented both allometrically corrected and raw indices, the latter of which are included here.

locomotor morphologies. The brachial (Fleagle, 1977) and crural (calculated from tibia and femur means published in Strasser, 1992) indices are greater in *Presbytis melalophos* than in *Trachypithecus obscura*. In *P. melalophos*, suspensory and leaping behaviors are more frequent than in the closely related arboreal quadruped *T. obscura*. They are also higher in *Pithecia pithecia*, in which more frequent clinging and leaping behavior is found, than in the closely related arboreal quadruped *Chiropotes satanas* (Fleagle and Meldrum, 1988).

Tail length. Relatively longer tails are ordinarily characteristic of arboreal monkeys (Rollinson and Martin, 1981). Presumably, in the nonprehensile-tailed forms, longer tails facilitate balance during quadrupedalism in the more precarious arboreal habitat. When normalized to body length, however, a higher tail length:body length ratio was found in *C. aethiops* than in *C. mitis*. The occurrence of a relatively longer tail in vervets may compensate for the effect on stability of their relatively longer distal limb segments during locomotor progression in the trees (Rollinson and Martin, 1981) and for transition between canopy and ground (Anapol and Gray, 2003).

Sexual dimorphism and social behavior

The results of this study show greater ($P < 0.05$) body-weight sexual dimorphism in *C. mitis* than in *C. aethiops*, and are consistent with those published by Plavcan et al. (1995), in which regression residuals for canine crown height regressed on body-weight sexual dimorphism were slightly greater in *C. mitis* (0.492) than in vervets (0.434). These findings challenge the commonly held tenet that sexual dimorphism and terrestrial locomotion are highly positively correlated, thus contradicting an expectation that body-weight dimorphism would be significantly larger in the more terrestrial *C. aethiops*.

Although alternative interpretations of these results must be considered, one tenable hypothesis predicts that these interspecific differences in body-weight sexual dimorphism result from interspecific differences in social organization (Plavcan et al., 1995; Plavcan and van Schaik, 1997), rather than differences in locomotor modality. Vervets live in relatively stable multimale, multifemale groups; often one adult male occupies a dominant or "alpha" role among the males (Fedigan and Fedigan, 1988). This organization corresponds most closely to the highest intensity intermale competition, "level 4," described by Kay et al. (1988), which would predict the highest degree of sexual dimorphism. In fact, the body-weight dimorphism of the current vervet sample ($m/f \approx 1.54$) exceeds that for all level 4 species in Kay et al. (1988), except for *Alouatta caraya* ($m/f \approx 1.557$), which is negligibly larger.

By contrast, mating in *Cercopithecus mitis* varies from a "female defense polygyny" pattern, in which one male monopolizes several females by aggres-

sively excluding other males, to promiscuous mating during multimale influxes (Cords, 1988). Body-weight dimorphism in *C. mitis* ($m/f \approx 1.87$) is greater than in most *Cercopithecus* species for which body weights have been published (Table 3) (Jungers, 1985; Leigh, 1992; Strasser, 1992; Fleagle, 1999). At least one other highly dimorphic cercopithecine, *Cercopithecus diana*, which is one of the more strict arborealists among guenons (Manaster, 1979; McGraw, 1996), also has a mating system that entails multimale influxes resulting in a breakdown of the one-male group structure and promiscuous mating (Cords, 1988, after Curtin, unpublished data). Although the polygynous model would imply low sexual dimorphism concomitant with little or no male competition, the high dimorphism found in both *C. mitis*, in this study, and in *C. diana* could possibly indicate a level of competition during multimale influx even greater than levels that normally occur in multimale, multifemale groups.

Evolutionary implications

Because most of the findings in the present study are consistent with a dichotomy between tree and ground locomotion, the temptation exists to perceive "semiterrestrialism" simply as engaging in, or adapting to, both arboreal and terrestrial activities. This perception, however, ignores the functional requirements associated with habitual transitions between trees and ground (Anapol and Barry, 1996; Anapol and Gray, 2003; Anapol et al., 2004). Broad categorical designations such as "arboreal," "terrestrial," and "semiterrestrial" may not accurately reflect the "totipotentiality" (Prost, 1965) of an animal's behavior. True "semiterrestriality," in fact, may not be merely sporadic mode shifting between arboreality and terrestriality, but rather a separate locomotor category with substantive morphological requirements in order to accommodate transitions between the two substrates. Relative percentages of climbing and/or leaping that may be included in the locomotor repertoire of ordinarily walking and running quadrupedal primates may be overlooked in the morphologies of both arboreal and terrestrial forms, as may relative proportions of arboreality and terrestriality in so-called "semiterrestrial" species. For example, although *C. ascanius* and *C. mitis* can both be classified as "arboreal quadrupeds," the propensity for red-tailed monkeys to leap more but climb less than blue monkeys (Gebo and Chapman, 1995) may account for significant differences between them, e.g., in intermembral and brachial indices (Gebo and Sargis, 1994). Vervets climb 29.5% of their locomotor time (Rose, 1979), more (McGraw, 1996) or nearly as much as (Gebo and Chapman, 1995) more arboreal cercopithecines and colobines. Vervets also leap 9.6% of their locomotor time (Rose, 1979), roughly as much as several more arboreal cercopithecids (McGraw, 1996). Thus, limb proportions of an arboreal monkey may skew from those of strictly terrestrial monkeys (Rodman, 1979) towards

those of climbers or leapers. Consequently, interpreting the body shape of a "semiterrestrial" monkey simply as a mosaic of features underlying both arboreality and terrestriality may obscure the importance of climbing and/or leaping for the transition between trees and ground.

CONCLUSIONS

- 1) Semiterrestrial vervets show limb proportions more usually associated with ground cursoriality than do blue monkeys. An exception to this convention is the relatively longer tails of vervets, which may compensate for any loss of balance, while in the trees, due to significantly greater brachial and crural indices. Although relative body length (\approx skeletal trunk length) is unexpectedly higher in the much larger blue monkeys, selection seems to favor a shorter trunk in vervets to reduce instability between fore- and hindquarters during terrestrial running. The small body size may allow vervets to walk and run on large boughs in the canopy in a manner similar to ground locomotion. Similarly, the relatively long tail would compensate, in the trees, for balance lost from having the relatively long distal limb segments and short back length required for rapid terrestriality.
- 2) Patterns of sexual size dimorphism in blue monkeys and vervets do not conform to expected differences between strict arborealists and arboreal species that spend more time in a terrestrial environment. The effect of differences in locomotor behavior on sexual size dimorphism may, in fact, be decoupled by the overriding impact of differences in social organization.
- 3) Broad, categorical generalizations about primate behavioral morphology must be tempered by how much of one or another locomotor mode is practiced (or niche is inhabited) relative to others. This additional input may dramatically affect the interpretation of results derived from nonspecific categories such as "semiterrestrial" or "semibrachiation" (Mittermeier and Fleagle, 1976). Other nonhabitual locomotory choices, e.g., leaping and/or climbing in arboreal and terrestrial quadrupeds, substrate transitions (e.g., between ground and trees), and nonlocomotor-related influences, such as social organization, must also be included in the interpretation of skeletal morphology.

ACKNOWLEDGMENTS

We express our grateful appreciation to John G. Fleagle and two anonymous reviewers for valuable comments and suggestions regarding the manuscript. Special thanks go to N.C. Dracopoli and J.G. Else for their assistance in Kenya.

LITERATURE CITED

- Anapol F, Barry K. 1996. Fiber architecture of the extensors of the hindlimb in semiterrestrial and arboreal guenons. *Am J Phys Anthropol* 99:429–447.
- Anapol F, Gray JP. 2003. Fiber architecture of the intrinsic muscles of the shoulder and arm in semiterrestrial and arboreal guenons. *Am J Phys Anthropol* 122:51–65.
- Anapol F, Shahnoor, N, Gray JP. 2004. Fiber architecture, muscle function, and behavior: gluteal and hamstring muscles of semiterrestrial and arboreal guenons. In: Anapol F, German RZ, Jablonski NG, editors. *Shaping primate evolution*. Cambridge: Cambridge University Press. p 99–133.
- Clutton-Brock TH, Harvey PH. 1977. Primate ecology and social organization. *J Zool Lond* 183:1–39.
- Cords M. 1988. Mating systems of forest guenons: a preliminary review. In: Gautier-Hion A, Bourliere F, Gautier J-P, Kingdon J, editors. *A primate radiation: evolutionary biology of the African guenons*. Cambridge: Cambridge University Press. p 323–339.
- Falsetti AB, Jungers WL, Cole TM III. 1993. Morphometrics of the callitricid forelimb: a case study in size and shape. *Int J Primatol* 14:551–572.
- Fedigan L, Fedigan L. 1988. *Cercopithecus aethiops*: a review of field studies. In: Gautier-Hion A, Bourliere F, Gautier J-P, Kingdon J, editors. *A primate radiation: evolutionary biology of the African guenons*. Cambridge: Cambridge University Press. p 389–411.
- Fleagle JG. 1977. Locomotor behavior and skeletal anatomy of sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). *Yrbk Phys Anthropol* 20:440–453.
- Fleagle JG. 1985. Size and adaptation in primates. In: Jungers WL, editor. *Size and scaling in primate biology*. New York: Plenum Press. p 1–19.
- Fleagle JG. 1999. *Primate adaptation and evolution*, 2nd ed. San Diego: Academic Press.
- Fleagle JG, Meldrum DJ. 1988. Locomotor behavior and skeletal morphology of two sympatric pitheciine monkeys, *Pithecia pithecia* and *Chiropotes satanas*. *Am J Primatol* 16:227–249.
- Gambarayan PP. 1974. *How mammals run*. New York: John Wiley.
- Gebo DL, Chapman CA. 1995. Positional behavior in five sympatric Old World monkeys. *Am J Phys Anthropol* 97:49–76.
- Gebo DL, Sargis EJ. 1994. Terrestrial adaptations in the postcranial skeletons of guenons. *Am J Phys Anthropol* 93:341–371.
- Hildebrand M. 1974. *Analysis of vertebrate structure*. New York: John Wiley and Sons.
- Hurov JR. 1987. Terrestrial locomotion and back anatomy in vervets (*Cercopithecus aethiops*), and patas monkeys (*Erythrocebus patas*). *Am J Primatol* 13:297–311.
- Jenkins FA Jr. 1974. Tree shrew locomotion and the origins of primate arborealism. In: Jenkins FA, editor. *Primate locomotion*. New York: Academic Press. p 85–115.
- Jorde LB, Spuhler JN. 1974. A statistical analysis of selected aspects of primate demography, ecology and social behavior. *J Anthropol Res* 30:119–224.
- Jungers WL. 1985. Body size and scaling of limb proportions in primates. In: Jungers WL, editor. *Size and scaling in primate biology*. New York: Plenum Press. p 345–381.
- Jungers WL. 1988. Relative joint size and hominoid locomotor adaptations with implications for the evolution of hominid bipedalism. *J Hum Evol* 17:247–265.
- Jungers WL, Falsetti AB, Wall CE. 1995. Shape, relative size, and size-adjustments in morphometrics. *Yrbk Phys Anthropol* 38:137–161.
- Kay RF, Plavcan JM, Glander KE, Wright PC. 1988. Sexual selection and canine dimorphism in New World monkeys. *Am J Phys Anthropol* 77:385–397.
- Kingdon J. 1974. *East African mammals: an atlas of evolution in Africa*. Volume 1. Chicago: University of Chicago Press. p 212.
- Larson SG. 1998. Unique aspects of quadrupedal locomotion in primates. In: Strasser E, Fleagle JG, McHenry H, Rosenberger A, editors. *Primate locomotion: recent advances*. New York: Plenum Press. p 157–174.

- Leigh S. 1992. Patterns of variation in the ontogeny of primate body size dimorphism. *J Hum Evol* 23:27–50.
- Lovich JE, Gibbons JW. 1992. A review of techniques for quantifying sexual size dimorphism. *Growth Dev Aging* 56:269–281.
- Majoral M, Berge C, Casinos A, Jouffroy FK. 1997. The length of the vertebral column of primates: an allometric study. *Folia Primatol (Basel)* 68:57–76.
- Manaster BJ. 1979. Locomotor adaptations within the *Cercopithecus* genus: a multivariate approach. *Am J Phys Anthropol* 50:169–182.
- McGraw WS. 1996. Cercopithecoid locomotion, support use, and support availability in the Tai Forest, Ivory Coast. *Am J Phys Anthropol* 100:507–522.
- McGraw WS. 2002. Diversity of guenon positional behavior. In: Glenn M, Cords M, editors. *The guenons: diversity and adaptation in African monkeys*. New York: Kluwer Academic/Plenum. p 113–131.
- Mittermeier RA, Fleagle JG. 1976. The locomotor and postural repertoires of *Ateles geoffroyi* and *Colobus guereza*, and a re-evaluation of the locomotor category semibrachiation. *Am J Phys Anthropol* 45:235–255.
- Mosimann JE. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. *J Am Stat Assoc* 65:930–945.
- Plavcan JM, van Schaik CP. 1997. Intrasexual competition and body weight dimorphism in anthropoid primates. *Am J Phys Anthropol* 103:37–68.
- Plavcan JM, van Schaik CP, Kappeler PM. 1995. Competition, coalitions and canine size in primates. *J Hum Evol* 28:245–276.
- Prost JH. 1965. A definitional system for the classification of primate locomotion. *Am Anthropol* 67:1198–1124.
- Rodman PS. 1979. Skeletal differentiation of *Macaca fascicularis* and *Macaca nemestrina* in relation to arboreal and terrestrial quadrupedalism. *Am J Phys Anthropol* 51:51–62.
- Rollinson L, Martin RD. 1981. Comparative aspects of primate locomotion, with special reference to arboreal cercopithecines. *Symp Zool Soc Lond* 48:377–427.
- Rose MD. 1979. Positional behavior in natural populations: some quantitative results of a field study of *Colobus guereza* and *Cercopithecus aethiops*. In: Morbeck ME, Preuschoft H, Gomberg N, editors. *Environment, behavior, and morphology*. New York: Gustav Fischer. p 75–94.
- Schultz AH. 1929. The technique of measuring the outer body of human fetuses and of primates in general. *Contrib Embryol* 20:213–258.
- Smith RJ. 1984. Determination of relative size: the “criterion of subtraction” problem in allometry. *J Theor Biol* 108:131–142.
- Smith RJ. 1999. Statistics of sexual dimorphism. *J Hum Evol* 36:423–458.
- Sneath PHA, Sokal RR. 1973. *Numerical taxonomy*. San Francisco: W.H. Freeman.
- Sokal RR, Rohlf FJ. 1981. *Biometry*, 2nd ed. San Francisco: W.H. Freeman.
- Strasser E. 1992. Hindlimb proportions, allometry, and biomechanics in Old World monkeys (Primates, Cercopithecidae). *Am J Phys Anthropol* 87:187–213.
- Turner TR, Mott CS, Maiers J. 1986. Genetic and morphological studies on two species of Kenyan monkeys, *C. aethiops* and *C. mitis*. In: Else JG, Lee PC, editors. *Primate evolution, proceedings of the Xth International Congress of Primatology*, Cambridge. London.
- Turner TR, Anapol F, Jolly CJ. 1997. Growth, development, and sexual dimorphism in vervet monkeys (*Cercopithecus aethiops*) at four sites in Kenya. *Am J Phys Anthropol* 103:19–35.
- Vangor A. 1979. Muscle function in an evolving primate ungulate, *Erythrocebus patas*. *Am J Phys Anthropol* 50:488 [abstract].