

## Positional Behavior in Five Sympatric Old World Monkeys

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**ABSTRACT** Observations of positional behavior and habitat use were recorded on focal individuals of five species of Old World monkeys at Kibale Forest, Uganda, through the dry season of 1990 and 1991. *Cercopithecus ascanius*, *Cercopithecus mitis*, *Cercocebus albigena*, *Colobus badius*, and *Colobus guereza* commonly utilize five similar types of positional behavior (i.e., quadrupedalism, leaping, climbing, sitting, and standing), but in varying frequencies and situations. As a group, colobines use oblique supports and leap more often, and cover greater linear distances during leaps than do cercopithecines. Colobines also prefer to sit (about 90% of all postures), while cercopithecines stand more frequently. Body size differences between the sexes of a species are not reflected in positional behavior. The two small-bodied species climb more and leap less often than the three larger species, which is the reverse of what we would expect. Leaping is the most common method of crossing open spaces within the canopy; but most spatial gaps and leaps are over short distances, usually one meter or less. All five species, regardless of body size or the availability of forest supports, prefer medium-sized supports. Incorporating our work from Uganda with previous investigations of positional behavior reveals few consistent trends with respect to body size or habitat use across primates. © 1995 Wiley-Liss, Inc.

Following Fleagle and Mittermeier's (1980) study on platyrrhine locomotor behavior, we proposed to study five sympatric species of Old World monkeys inhabiting Kibale Forest, Uganda. Our hopes were similar to theirs in our attempt to add to the relatively scant body of locomotor and postural data on primates of differing body sizes, and on sympatric species utilizing the same area of the primary forest within a single season. This approach minimizes the potential effect of differences in forest structure and seasons on positional behavior. Old World monkeys are a good group in which to conduct such a comparative study, since all five species are contained within a single taxonomic family (Cercopithecidae), thus reducing phylogenetic effects. We compared two species of guenons, *Cercopithecus ascanius* and *Cercopithecus mitis*, and one man-

gabey, *Cercocebus albigena*, within Cercopithecinae, with two colobines, *Colobus badius* and *Colobus guereza*. This project attempted to identify the distinctiveness of each of these five cercopithecoid species and to understand the relationships between positional behavior, body size, and habitat utilization among them. We expected that as body size increased, climbing, substrate size, and vertical and oblique support use would also increase. We further expected smaller animals to show increased leaping frequencies and decreased use of the mid- and upper canopy. The work of Cartmill (1974, 1985), Cartmill and Milton (1977),

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TABLE 1. Mean values for tree characteristics of the ten most common trees in Kibale Forest, Uganda ( $n = 5$  for each species)

	DBH	TH	CV	MH	MO	MV	LH	LO	LV
1. <i>Diospyros abyssinica</i>	33.1	26.4	1,034	11.5	19.0	0.1	2.9	7.0	1.4
2. <i>Markhamia platycalyx</i>	45.9	29.3	986	6.2	16.6	0.2	1.6	4.6	1.2
3. <i>Celtis durandii</i>	38.6	23.7	1,343	4.6	15.6	0.9	1.6	6.1	1.8
4. <i>Uvariopsis congensis</i>	21.3	15.4	431	8.4	12.2	1.0	0.2	0.8	1.6
5. <i>Bosqueia phoberos</i>	21.4	12.4	488	5.4	10.4	1.2	0.6	1.6	0.8
6. <i>Funtumia latifolia</i>	41.2	33.3	1,054	10.0	24.0	2.0	1.8	3.2	1.6
7. <i>Teclea nobilis</i>	21.3	13.0	683	3.4	14.6	1.2	0.0	4.2	2.4
8. <i>Chaetacme aristata</i>	44.7	12.6	990	12.2	18.4	5.8	2.4	4.4	3.0
9. <i>Strombosia scheffleri</i>	66.7	23.2	2,388	9.6	22.2	1.2	7.6	6.6	1.6
10. <i>Trema orientalis</i>	49.5	24.6	5,932	12.6	27.4	2.8	3.4	9.6	1.8
Combined hypothetical tree	38.4	21.4	1,533	8.4	18.0	1.6	2.2	4.4	1.7

DBH = diameter at breast height, cm; TH = tree height, m; CV = canopy volume, m<sup>3</sup>; MH = number of medium-sized horizontal branches; MO = number of medium-sized oblique branches; MV = number of medium-sized vertical branches; LH = number of large-sized horizontal branches; LO = number of large-sized oblique branches; LV = number of large-sized vertical branches.

Jungers (1978, 1979, 1985), Grand (1984), Fleagle (1978, 1985), Fleagle and Mittermeier (1980), and Cant (1987a,b, 1992) strongly support these expectations on mechanical as well as naturalistic observations (but see Crompton, 1984). Thus, we expected *Cercopithecus ascanius*, the smallest monkey in our study, to leap more often and climb less often than the largest monkey, *Colobus guereza*. Further, since the five species span a range of increasing body sizes from 3.6 to 9.1 kg, we expected trends of increasing or decreasing frequencies for climbing and leaping relative to body size. Napier (1967), Cartmill (1974), Fleagle (1976, 1978, 1980, 1985), Fleagle and Mittermeier (1980), Crompton (1984), Cant (1987a,b, 1992), and Garber (1992) have suggested that differences in body size may alter an organism's use of the arboreal milieu, and some have stated that primate locomotion is specifically tied to certain forest levels (Charles-Dominique, 1977; MacKinnon and MacKinnon, 1978; Fleagle, 1976, 1978; Fleagle and Mittermeier, 1980). Thus, we also expected that body size might dictate where or how a species uses the structural parts of a tree (e.g., canopy height, support sizes, or major branches). In all, we planned to test these expectations with five sympatric arboreal Old World monkeys which are largely quadrupedal and contained within a single taxonomic family.

This information was also collected in the hope that data of this type will be useful to morphologists in their attempt to relate behavior with morphology, as well as for ecologists

trying to understand habitat use. Our ultimate objective was to incorporate our work from Kibale Forest with previously published results in an attempt to discover trends within primate positional behavior with respect to size, habitat, and morphology.

## METHODS

### Environment

The Kibale Forest Reserve, located in western Uganda (0° 13'–0° 41' N and 30° 19'–30° 32' E) near the base of the Ruwenzori Mountains, is a moist, evergreen forest (Wing and Buss, 1970; Struhsaker, 1975; Kasenene, 1980; Skorupa, 1986, 1988; Kalina, 1988). The reserve is 560 km<sup>2</sup> and about 60% of Kibale Forest is characterized by tall forest with the canopy generally 25–30 m high (Butynski, 1990), although some trees may exceed 55 m. The remainder of the reserve is comprised of a mosaic of swamp, grassland, plantations of pine, thicket, and colonizing forest (Wing and Buss, 1970; Butynski, 1990). The study site, Kanyawara, is situated at an elevation of 1500 m. All observations were made within the K-14 forest compartment. Throughout the Kanyawara area trees such as *Diospyrus abyssinica* (12.3% of 2,111 enumerated trees), *Markhamia platycalyx* (11.8%), *Celtis durandii* (10.9%), *Uvariopsis congensis* (9.8%), and *Bosqueia phoberos* (8.7%) are common (Table 1). Mean annual rainfall (1987–1990) has averaged 1,709.5 mm (range = 1,607–1,839 mm). The annual mean daily mini-

TABLE 2. Species studied at Kibale Forest, Uganda, and the nature of the sample of locomotor bouts collected<sup>1</sup>

	<i>C. ascanius</i>	<i>C. mitis</i>	<i>C. albigena</i>	<i>C. badius</i>	<i>C. guereza</i>
Body weight (g)					
Males	4,170	6,000	8,980	8,250	10,100
Females	3,000	3,500	6,400	8,240	8,040
Male/female ratio	1.4	1.7	1.4	1.0	1.3
Mean weight (g)	3,585	4,750	7,960	8,245	9,070
Total bouts	6,450	6,444	6,165	7,515	6,452
Locomotor bouts	3,653	3,413	3,911	4,949	4,143
Postural bouts	2,797	3,031	2,254	2,566	2,309
Contact hours	59	46	69	97	131
Minutes/switch	15.9	14.9	15.7	13.3	23.5
Day range (km)	1.4	1.3	1.3	0.6	0.5

<sup>1</sup> Body weights from Waser (1987) and Fleagle (1988). Day range values from Struhsaker (1978) and Struhsaker and Leland (1979) for *C. ascanius*, *C. albigena*, and *C. badius*; from Rudran (1978) and Struhsaker (1978) for *C. mitis*; from Oates (1977) and Struhsaker (1978) for *C. guereza*.

mum temperature (1977–1983) was  $16.2 \pm 0.4^\circ\text{C}$ , while the maximum averaged  $23.3 \pm 0.6^\circ\text{C}$  (Butynski, 1990).

Five individuals of the ten most common trees in Kanyawara were measured to determine the diameter at breast height, tree crown, crown volume, and the number of large and medium-sized branches according to their orientation (horizontal, oblique, or vertical) (Table 1). These measurements were collected to reflect the average types of potential supports primates encounter within the forest. Two 600 meter transects were walked to determine the number and length of the spatial gaps between adjacent trees.

### Sampling methods

Positional behavior was recorded on five species of Old World monkeys (*Cercopithecus ascanius*, *Cercopithecus mitis*, *Cercocebus albigena*, *Colobus badius*, and *Colobus guereza*) inhabiting Kibale Forest during the dry season (May–August) in 1990 and in 1991. All of these species were relatively well habituated to observers, although no species was observed closer than 3 m. However, black and white colobus were still wary and we believe this may have biased our canopy height data in favor of the upper canopy. Most individuals in all five species settled down to their normal regime after an initial moment of uncertainty. A focal animal technique of continuous sampling adults was used (Altmann, 1974). The focal animal approach maximizes the collection of sequential behavior, in particular movement sequences, and thus helps to answer

the question of what does an individual animal do when it moves. Switching between focal animals occurred frequently since few animals were collared or distinctively marked, and moving animals could be lost from view. The amount of switching and the mean time of observation for individuals within a species are documented in Table 2. More than 20 individuals were sampled for each species.

Positional behavior bouts were recorded in the context of an associated behavior, the physical structure used (size and orientation), and the location of the supports (canopy height). A bout is defined as a change in positional behavior (see Fleagle, 1976; Fleagle and Mittermeier, 1980; Susman, 1984; Gebo, 1992). Adult animals were observed continuously from first contact until approximately 500 positional bouts were recorded for that particular day (between 7 and 9 hours of observation). Hours of observation as well as total bouts are listed in Table 2. Unlike more complex socioecological behaviors, positional behavior is fairly stereotypic and after about 3,000 bouts, only minor changes seem to occur in the frequencies (e.g., a 1–3% change for quadrupedalism, leaping, or climbing over the next 3,000 bouts within a given season and forest type; Fig. 1). Thus, total bouts may be more indicative of a sampling regime than total hours of observation. A goal of 6,500 bouts was set for each species (Table 2).

Separating certain activities (i.e., foraging for insects versus travel within a tree) was extremely difficult in certain situations, so we felt it best to score activities within the

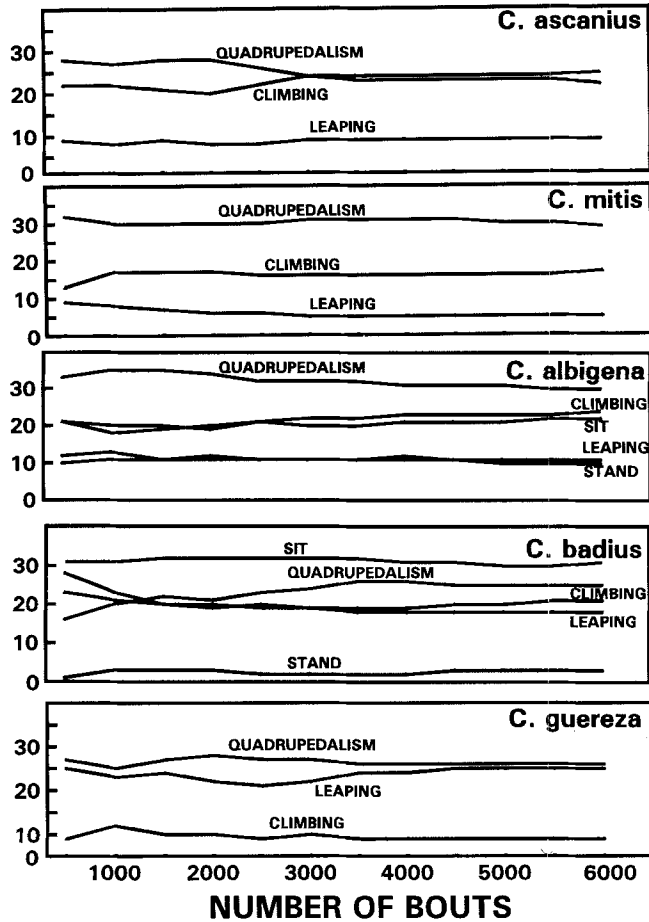


Fig. 1. Cercopithecine and colobine frequencies of positional behavior over 500 bout intervals.

context of a single tree or between trees. Positional behavior was scored as travel when movement occurred between trees. Positional behavior within a single tree includes feeding, foraging, and resting. The activity resting represents postures of generally longer time duration, but each was scored as a single bout regardless of the length of time involved.

Table 3 lists and defines the locomotor, postural, and environmental variables recorded. Most of the locomotion and postures for Old World monkeys are described and illustrated in Ripley (1967), Morbeck (1975), Mittermeier and Fleagle (1976), Fleagle (1978, 1980), and Rose (1979). For leaps, the orientation of the take-off and landing sup-

port were recorded, as well as the horizontal and vertical distances traveled in terms of body lengths (Table 4). Estimated mean head and body length measurements for the five species (sexes combined) are 574 cm for *Colobus guereza*, 533 cm for *Colobus badius*, 540 cm for *Cercocebus albigena*, 442 cm for *Cercopithecus ascanius*, and 473 cm (estimate) for *Cercopithecus mitis* (Hadow, 1952; Napier and Napier, 1967).

We recorded positional behaviors which we perceived might be of adaptive concern from a morphologist's perspective. Thus, we lumped positional variables of the same variety. For example, the posture sitting was lumped and scored as one variable instead of dividing it into a variety of sitting types as

TABLE 3. *Locomotor, postural, and substrate variables***Locomotion**

Q = quadrupedalism: a movement in which all four limbs move in a regular pattern above a support or on the ground; walking, running, and galloping are recorded as quadrupedalism

L = leaping: a movement in which the hindlimbs propel an animal across a gap; leaping included quadrupedal standing then leaping or pumping the body up and down before leaping, vertical clinging and then leaping, and quadrupedal running and leaping; dropping down from a branch was not scored as a leap; distances of leaps were estimated using head and body lengths excluding tail length

CL = climbing: 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 often 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. Although some authors (e.g., Cant, 1987b, 1988) prefer to break up this category, it is not so clearly demonstrated in observations in the field that vertical climbing is always such a regularly paced and uniform motion akin to quadrupedalism (e.g., vertical climbing along non-vertical supports) nor is it different in "body orientation or patterns of limb use" (Cant, 1987b, p. 74). Thus, we prefer to lump these behaviors within climbing. We also have chosen to report our vertical climbing frequencies within the text and this will allow individuals to separate the amount of scrambling/clambering variety of climbing from the vertical variety

QS = quadrupedal suspensory movements: a movement in which the body is progressing below a support using three or four limbs

BR = bridging: a movement where spatial gaps are crossed by body stretching; first, the hands stretch out and grab the new and distant support and then the body is stretched across and then pulled over from the old to the new support

BM = bimanualism: a movement in which the hands grasp a support and are used to pull the body up to a support from below (bimanual pull-up)

BI = bipedalism: a movement in which only the hind feet are used to take a short walk

VB = vertical bounding: short successive jump-clings upward along a vertical support (see trunk climbing in Ripley, 1967, p. 159)

**Postures**

S = sitting: animal rests on its haunches; can sit with feet in toward the mid-line of the body or spread outward; can sit with feet above the head; can have feet grasping or hanging over the support or propping the body up with midfoot or heel touching the support

VCL = vertical clinging: animal clings to a vertical support without sitting on a branch

QSU = quadrupedal suspension: body of an animal is suspended underneath a support usually by all four limbs; three or four limb suspensions were scored quadrupedal suspension

SBM = suspend bimanually: suspend by arms, normally with bent elbows

HSU = hindlimb suspension: suspend by hindlimbs

ST = standing: animals stands on all four limbs

BIP = bipedal stand: animals stands on hindfeet, normally with the heel elevated above the support

RC = recline: animal lies down on its ventrum, its side, or its back

**Correlated behavior**

T = travel: long distance movements between trees; normally movements between a series of trees from or to feeding or resting sites (postures that are scored during travel are brief pauses between locomotor activities)

F = feed/forage: movements within a single tree

R = rest: periods of inactivity

**Support orientation**

H = horizontal support: 0 to 15 degrees to the horizontal

O = oblique support: between 15 and 75 degrees to the horizontal

V = vertical support: from 75 to 90 degrees to the horizontal

**Support sizes**

L = large support: more than 25 cm in circumference

M = medium-sized support: between 6 and 25 cm in circumference

S = small support: less than 5 cm in circumference

**Canopy height classes**

U = upper height zone: >16 to 30 m

M = middle height zone: 5 to 15 m

L = lower height zone: <5 m

has been done by other researchers (Fontaine, 1990; Hunt, 1992).

Doran (1992) tested a methodology used by Fleagle (1976) which modified locomotor frequencies by taking into account the mean distance of movement for each type of locomotion. This method compensates for the long distance movements documented

within a single locomotor bout relative to common shorter distance locomotor behaviors. Thus, long distance movements like quadrupedalism during travel are emphasized via their higher mean distances compared to short distance movements like climbing. This is one way to weigh locomotor frequencies and in the process try to more

TABLE 4. *Leaping distances and substrate use*<sup>1</sup>

	N	Horizontal distance in body lengths									
		<1	1	2	3	4	5	6	7	8	9
<i>Cercopithecus ascanius</i>	500	10%	64%	16%	5%	3%	1%	<1%	0%	<1%	0%
<i>Cercopithecus mitis</i>	322	16	57	21	4	1	0	0	0	0	0
<i>Cercocebus albigena</i>	426	20	55	18	5	1	<1	0	0	0	0
<i>Colobus badius</i>	1,063	7	46	25	11	8	1	1	0	<1	0
<i>Colobus guereza</i>	927	15	52	18	9	4	1	<1	0	0	0

	N	Vertical descent in body lengths									
		<1	1	2	3	4	5	6	7	8	9
<i>Cercopithecus ascanius</i>	376	45%	30%	9%	8%	3%	2%	2%	<1%	<1%	<1%
<i>Cercopithecus mitis</i>	350	52	28	10	5	3	1	1	<1	0	0
<i>Cercocebus albigena</i>	341	50	29	11	6	3	2	1	0	0	0
<i>Colobus badius</i>	871	20	36	20	9	8	2	2	1	1	1
<i>Colobus guereza</i>	897	26	48	14	6	4	1	<1	<1	0	0

	N	Substrate use (from/to supports)								
		HH	HO	HV	OH	OO	OV	VH	VO	VV
<i>Cercopithecus ascanius</i>	500	36%	9%	1%	10%	40%	4%	1%	1%	<1%
<i>Cercopithecus mitis</i>	323	51	11	3	6	27	1	1	1	0
<i>Cercocebus albigena</i>	576	49	10	4	6	24	1	3	1	2
<i>Colobus badius</i>	1,110	37	9	2	5	42	1	1	1	1
<i>Colobus guereza</i>	903	45	6	1	4	40	2	1	1	<1

<sup>1</sup>N = sample size; <1 through 9 represent the number of body lengths for each leap; horizontal distance = the linear distance of a leap from take-off to landing; vertical descent = the distance downward from take-off to landing; H = horizontal support; O = oblique support; V = vertical support; HH = a leap from a horizontal support to a horizontal support.

accurately reflect selective pressures on morphology, although short powerful movements like leaping may in fact cause greater peak stresses in primate limbs than walking long distances. For the five monkey species at Kibale Forest, quadrupedalism during travel, due to its high mean distance values (Table 5), shows the highest frequency modifications from the reported raw frequencies (Table 6). Mean distances across species, locomotor type, and activity at Kibale Forest are, however, generally similar, and thus, the pattern of use by these five species is similar to the unadjusted values. Modified frequencies only tended to accentuate key movement differences (Table 6). Thus, we decided to simply note what the modified frequencies would be (Table 6) and to report the unmodified frequencies (percent of bouts) throughout this manuscript.

In the second field season (1991), 10 minute scans were recorded to count individuals in the crown, major branches, or trunks of trees (Table 7). Likewise, locomotor distances in body lengths (<1 to 10+) for quadrupedalism, climbing, and leaping were recorded with their associated behav-

ior (travel = between tree; feed = within tree; Table 5).

### Statistical methods

Analyses of locomotor data are difficult because the behavior performed at one point in time is dependent on the behavior just performed. Scan sampling does not eliminate this problem because animals may use one postural category for a number of successive scans and thus defining independent sampling units is extremely difficult (see Dagosto, 1994). Since, the majority of the previous work in this field has simply ignored this problem, we initially follow suit and simply report the profile for each species calculated from all observations, and contrast the percentages in a qualitative manner. Thus, raw frequencies (percent of bouts) are reported throughout the manuscript. However, to statistically analyse this data and to consider the problem of interdependence, we took two approaches. First, we divided the entire data set into 100 bout segments, and for each segment, we determined a locomotor profile. Subsequently, we systematically removed every second 100 bout

TABLE 5. Distance covered by quadrupedalism (Q), climbing (CL), and leaping (L) in body lengths (<1 to 10+) during travel (T) and feeding (F)<sup>1</sup>

	N	<1	1	2	3	4	5	6	7	8	9	10+	Mean distance
<i>Cercopithecus ascanius</i>													
QF	720	10%	52%	26%	8%	3%	<1%	<1%	<1%	0%	0%	0%	1.5
QT	311	<1	12	23	19	20	7	6	4	4	1	3	3.7
CLF	478	27	54	17	2	<1	0	0	0	0	0	0	1.1
CLT	240	13	33	40	18	5	0	0	0	0	0	0	1.9
LF	272	12	64	15	5	3	1	1	0	0	0	0	1.3
LT	278	8	65	18	6	2	1	<1	0	0	0	0	1.4
<i>Cercopithecus mitis</i>													
QF	696	12	55	22	6	3	1	<1	<1	0	<1	0	1.4
QT	248	0	10	28	16	18	9	7	7	3	1	2	3.7
CLF	467	23	59	15	3	<1	<1	0	0	0	0	0	1.1
CLT	196	1	34	39	18	7	2	0	0	0	0	0	2.0
LT	112	23	64	12	1	0	0	0	0	0	0	0	0.9
LT	249	13	55	25	6	2	0	0	0	0	0	0	1.3
<i>Cercocebus albigena</i>													
QF	706	7	53	26	8	4	1	1	0	0	0	<1	1.6
QT	344	<1	10	23	19	22	10	7	4	2	1	1	3.6
CLF	437	23	57	16	2	1	0	0	0	0	0	0	1.1
CLT	254	12	33	35	20	7	2	1	0	0	0	0	2.1
LF	160	29	55	11	3	2	0	0	0	0	0	0	0.9
LT	499	16	55	22	6	1	<1	0	0	0	0	0	1.2
<i>Colobus badius</i>													
QF	744	12	42	27	11	3	2	1	<1	<1	0	0	1.6
QT	302	1	10	25	20	18	9	7	3	2	1	2	3.4
CLF	481	27	47	17	6	2	1	<1	0	<1	0	0	1.3
CLT	224	2	21	38	24	9	3	2	<1	<1	0	0	2.4
LF	334	24	54	15	4	2	1	1	0	1	0	0	1.1
LT	566	10	55	13	10	5	2	3	1	0	0	0	1.7
<i>Colobus guereza</i>													
QF	853	9	45	26	9	5	1	1	<1	<1	<1	<1	1.7
QT	421	0	4	14	12	18	12	15	6	4	4	9	4.9
CLF	631	21	50	19	7	2	<1	<1	0	0	0	0	1.3
CLT	278	0	15	35	23	12	5	4	2	1	1	0	2.8
LF	268	27	46	15	10	2	<1	0	0	0	0	0	1.3
LT	525	11	50	23	10	5	1	<1	0	0	0	0	1.6

<sup>1</sup> N = number of observations; <1 to 10+ represents the number of body lengths (linear distance) covered for each movement and is reported in percent used; Mean distance = mean body lengths for each movement; QF = quadrupedalism during feeding; QT = quadrupedalism during travel; CLF = climbing during feeding; CLT = climbing during travel; LF = leaping during feeding; LT = leaping during travel.

segment and used each second unit in statistical comparisons between species and positional behavior. Thus, every second segment was considered to be independent (e.g., 0–100 was independent of 200–300) and the intermediate data was discarded. Secondly, we simply ignored the issue of independence, and report comparisons between every 100 bout segment (e.g., 0–100 was considered to be independent of 101–200). By reporting both comparisons, the reader can evaluate the implications of independence relative to the reduced sample size resulting from the data removal. We tested each group with an analysis of variance, and examined individual pairwise differences using a Scheffé test. The Scheffé test allows us to contrast all possible pairs of group means from our analysis of variance to make post

hoc comparisons. For instance, if an overall difference was found in the frequency use of positional behavior, we examined where this difference occurred (i.e., between *mitis* and *ascanius*, between *mitis* and *badius*, etc.). We selected the Scheffé test since it uses a single range for all comparisons and it is quite conservative compared to other post hoc tests. Thus, to attain significance, differences have to be rather substantial. Table 8 reports the results of this analysis and we refer to Table 8 within the text when statistical significance is apparent.

## RESULTS

### Sex differences

Comparing male and female locomotor frequencies across species and activities

TABLE 6. Positional behavior by activity—travel vs. feeding<sup>1</sup>

	N	Locomotor frequencies							
		Q	L	CL	QS	BR	BM	BI	VB
<i>Cercopithecus ascanius</i>									
Travel	1,124	41%	25%	27%	0%	<1%	<1%	0%	7%
Feed	2,529	38	11	50	0	1	<1	0	1
<i>Cercopithecus mitis</i>									
Travel	1,367	51	18	29	<1	<1	<1	0	1
Feed	2,046	55	6	38	0	<1	<1	0	<1
<i>Cercocebus albigena</i>									
Travel	2,328	46	21	31	0	<1	1	<1	<1
Feed	1,583	48	11	40	<1	<1	1	<1	<1
<i>Colobus badius</i>									
Travel	3,204	34	30	29	<1	0	3	<1	3
Feed	1,745	44	16	37	<1	0	2	0	1
<i>Colobus guereza</i>									
Travel	2,056	39	44	11	<1	0	<1	0	5
Feed	2,087	43	33	18	0	0	1	<1	4
		Modified locomotor frequencies (after Doran, 1992)							
		Q	L	CL					
<i>Cercopithecus ascanius</i>									
Travel		64%	22%	15%					
Feed		45	11	44					
<i>Cercopithecus mitis</i>									
Travel		70	9	21					
Feed		62	4	34					
<i>Cercocebus albigena</i>									
Travel		65	10	25					
Feed		59	8	34					
<i>Colobus badius</i>									
Travel		49	22	29					
Feed		52	13	35					
<i>Colobus guereza</i>									
Travel		65	24	11					
Feed		53	31	18					
		Postures							
	N	S	ST	RC	VCL	QSU	HSU	SBM	BIP
<i>Cercopithecus ascanius</i>									
Travel	488	72%	27%	0%	1%	0%	0%	0%	1%
Feed	2,309	69	25	<1	<1	<1	0	0	5
<i>Cercopithecus mitis</i>									
Travel	676	59	40	2	1	1	0	0	1
Feed	2,355	65	29	2	0	0	0	0	3
<i>Cercocebus albigena</i>									
Travel	740	56	41	1	1	<1	0	0	<1
Feed	1,514	71	23	3	<1	<1	<1	<1	2
<i>Colobus badius</i>									
Travel	995	88	11	<1	1	<1	0	<1	0
Feed	1,571	91	7	1	<1	0	0	<1	1
<i>Colobus guereza</i>									
Travel	554	94	5	1	1	0	0	0	0
Feed	1,730	86	4	10	<1	<1	0	<1	<1

<sup>1</sup>Abbreviations as in Table 3.

(travel versus feed) shows quadrupedalism to vary by no more than 2% between males and females across all five species (Table 9). Differences in climbing frequency is typically less than 2% by sex; however, for *C. albigena*, there was a 4% difference during feeding. Leaping frequencies by sex vary by

2% or less between *C. ascanius* and *C. mitis*, by 3% between *C. albigena* and *C. guereza* during feeding, and by 4% for *C. badius* during feeding (Table 9). Travel frequencies are extremely consistent across sex while the activity feeding shows somewhat larger differences. Overall, no appreciable locomotor



TABLE 7. Tree use by species in Kibale Forest, Uganda<sup>1</sup>

Species	Scans	N	Crown	Major branch	Trunk
<i>Cercopithecus ascanius</i>	122	388	62%	36%	2%
<i>Cercopithecus mitis</i>	122	486	60	40	<1
<i>Cercocebus albigena</i>	124	545	53	46	1
<i>Colobus badius</i>	125	846	65	33	2
<i>Colobus guereza</i>	124	468	28	72	0

<sup>1</sup> Scans = the number of recordings; N = number of observations for all scans; crown = animals located in the crown of a tree; major branch = animals located on a major branch of a tree; trunk = animals located on the trunk of a tree.

differences can be documented between males and females in these sexually dimorphic species, even though the sexes clearly differ in their respective body sizes (Table 2).

#### Support use by sex

All five species prefer medium-sized supports, and there are no large frequency differences between sexes, with the exception of *C. albigena* (Table 10). The smaller-sized females do use the largest supports slightly less often than do males of the same species, although this is not the case in *C. albigena*. Further, a decrease in use of large-sized supports by females is also evident in red colobus monkeys although mean body weights for males and females are generally similar. A slight increase in use of small supports is noted for females across species, especially in red-tailed and red colobus monkeys (Table 10). Overall, however, there is at best only slight evidence that body size differences due to sex account for frequency differences in support use.

#### Support orientation by sex

The use of differing support orientations (horizontal, oblique, or vertical) by the sexes appears to be very similar across all species (Table 10). The biggest difference between the sexes is observed in *C. guereza*, where females use oblique supports more frequently than do males, who prefer horizontal supports.

#### Canopy use by sex

Both males and females use the middle canopy more often than the upper canopy (Table 10), except for red colobus males and *C. guereza*, where the upper canopy is used more frequently. The lower canopy is used only

moderately by all species with the heaviest use by red colobus females and *C. ascanius*. Comparing only upper canopy use by males and females shows *C. mitis* and *C. guereza* to be consistent in their use of this zone, while males in *C. ascanius* and *C. badius* and females in *C. albigena* differentially use the upper canopy. In general, species differences due to sex show no consistent trend of canopy use.

#### SPECIES PROFILES

*Cercopithecus ascanius*, the red-tailed monkey, prefers to move using climbing (43%) and quadrupedalism (39%) (Table 11). Leaping represents only 15% of the locomotor profile. Most leaps are less than two body lengths in a horizontal or linear direction, although occasional leaps can span up to six body lengths in overall distance (Table 4; Fig. 2). Vertical bounding makes up 3% of the locomotor profile (Table 11). Other movements such as bridging, bimanualism, and quadrupedal suspensory movements are rarely used. At rest ( $n = 34$ ), *C. ascanius* sits (89%), stands (9%), and reclines (3%). *C. ascanius* prefers the mid-canopy and is usually found in the crown of a tree (Tables 7 and 12). Medium-sized horizontal and oblique supports are the most often utilized (Table 12). *C. ascanius* is considered to have an omnivorous diet with an emphasis on frugivory (Struhsaker, 1978; Struhsaker and Leland, 1979). It exhibits the highest plant diversity (80 species) in diet among Kibale Forest monkeys (Struhsaker, 1978).

*Cercopithecus mitis*, the blue monkey, is a frequent user of quadrupedalism (54%) and climbing (35%) (Table 11). Quadrupedal suspensory movements, bridging, bimanualism, and vertical bounding are rarely observed. Leaping represents 11% of the

TABLE 8. Statistical comparisons of positional behavior by species<sup>1</sup>

	1	2	3	4	5
<b>Quadrupedalism</b>					
1. <i>ascanius</i>					
2. <i>mitis</i>	*				
3. <i>albigena</i>		<u>*</u>			
4. <i>badius</i>	<u>*</u>		*		
5. <i>guereza</i>		*			
<b>Leaping</b>					
1. <i>ascanius</i>					
2. <i>mitis</i>	*				
3. <i>albigena</i>	<u>*</u>				
4. <i>badius</i>	<u>*</u>	<u>*</u>	<u>*</u>		
5. <i>guereza</i>	<u>*</u>	<u>*</u>	<u>*</u>	<u>*</u>	
<b>Climbing</b>					
1. <i>ascanius</i>					
2. <i>mitis</i>	<u>*</u>				
3. <i>albigena</i>	<u>*</u>				
4. <i>badius</i>	*	*			
5. <i>guereza</i>	<u>*</u>	<u>*</u>	<u>*</u>	<u>*</u>	
<b>Vertical bounding</b>					
1. <i>ascanius</i>					
2. <i>mitis</i>					
3. <i>albigena</i>					
4. <i>badius</i>					
5. <i>guereza</i>	<u>*</u>	<u>*</u>	<u>*</u>	<u>*</u>	
<b>Sitting</b>					
1. <i>ascanius</i>					
2. <i>mitis</i>					
3. <i>albigena</i>	<u>*</u>	<u>*</u>			
4. <i>badius</i>			<u>*</u>		
5. <i>guereza</i>			<u>*</u>		
<b>Vertical clinging (no statistical differences)</b>					
<b>Standing</b>					
1. <i>ascanius</i>					
2. <i>mitis</i>	<u>*</u>				
3. <i>albigena</i>	<u>*</u>				
4. <i>badius</i>	<u>*</u>	<u>*</u>	<u>*</u>		
5. <i>guereza</i>	<u>*</u>	<u>*</u>	<u>*</u>		
<b>Bipedal standing</b>					
1. <i>ascanius</i>					
2. <i>mitis</i>	*				
3. <i>albigena</i>	*	<u>*</u>			
4. <i>badius</i>	*	<u>*</u>			
5. <i>guereza</i>	<u>*</u>	<u>*</u>			
<b>Reclining</b>					
1. <i>ascanius</i>					
2. <i>mitis</i>					
3. <i>albigena</i>		*			
4. <i>badius</i>					
5. <i>guereza</i>	*	<u>*</u>	*	<u>*</u>	
<b>Bimanualism</b>					
1. <i>ascanius</i>					
2. <i>mitis</i>					
3. <i>albigena</i>					
4. <i>badius</i>	<u>*</u>	<u>*</u>	<u>*</u>		
5. <i>guereza</i>				<u>*</u>	

<sup>1</sup>An Analysis of Variance was performed to test whether individual pairwise differences were statistically significant using a Scheffe test. An asterisk represents a significant result at the 0.05 level of significance for the 100-bout division of the data set. Underlined asterisks represent statistically significant values after the removal of every other 100-bout interval.

96% of all postures. During rest (n = 152), *C. mitis* prefers to sit (57%), to stand (11%), and to recline (31%). Blue monkeys prefer horizontal and medium-sized supports as well as the mid-canopy (Table 12). Like *C. ascanius*, *C. mitis* is omnivorous with a preference for fruit in its diet and these species have the highest amount of dietary overlap among Kibale Forest monkeys, especially for arthropod prey (Struhsaker, 1978).

*Cercocebus albigena*, the grey-cheeked mangabey (which is sometimes placed within the genus *Lophocebus*, see Groves, 1978), has a locomotor profile similar to that of blue monkeys with quadrupedalism, 47%; climbing, 35%; and leaping, 15% (Table 11). When climbing, the grey-cheeked mangabey frequently uses vertical climbing sequences (15%) (Table 13). Although rare, bimanualism is observed more often in *C. albigena* than the guenons (Table 11). At rest (n = 325), *C. albigena* prefers to sit (73%), to stand (14%), and to recline (13%). *C. albigena* uses the mid-canopy most often, and prefers medium-sized and horizontal supports. *C. albigena* is chiefly a frugivore and is distinct from the guenons in its low intake of leafy or floral material (Struhsaker, 1978).

*Colobus badius*, the red colobus monkey, uses quadrupedalism, 37%; climbing, 32%; and leaping, 25% (Table 11). Bimanualism and vertical bounding are frequently observed in red colobus monkeys. Quadrupedal suspensory movements, bridging, and bipedalism are very rare. Quadrupedal suspensory movements are most often observed after leaps when animals misjudge or rotate over the branch and thus need to scramble on top of a branch to re-orient themselves. At rest (n = 291), *C. badius* definitely prefers to sit (93%), with standing (2%), and reclining (5%) showing much lower frequencies of use. *C. badius* equally prefers the upper and mid-canopy, as well as horizontal and oblique supports (Table 12). Medium-sized supports are, however, clearly preferred (67%, Table 12). *C. badius*, has a very folivorous diet compared to the cercopithecines and feeds on a large variety of different plant species, although concentrating on buds, young leaves, and petioles of mature leaves (Struhsaker and Oates, 1975; Struh-

locomotor profile and distances are generally less than two body lengths per leap (Table 4). Sitting and standing represent

TABLE 9. Locomotor behavior by species, by sex, and by activity<sup>1</sup>

	N	Q	L	CL	QS	BR	BM	BI	VB
<i>Cercopithecus ascanius</i>									
Travel									
Males	313	42%	26%	27%	0%	0%	<1%	0%	5%
Females	808	41	24	27	0	<1	<1	0	7
Feeding									
Males	686	38	12	48	0	1	1	0	0
Females	1841	38	10	50	0	1	<1	0	1
<i>Cercopithecus mitis</i>									
Travel									
Males	576	50	18	29	<1	<1	1	0	2
Females	789	51	18	29	0	<1	<1	0	1
Feeding									
Males	809	55	5	39	0	<1	<1	0	0
Females	1,236	56	6	37	0	<1	<1	0	<1
<i>Cercocebus albigena</i>									
Travel									
Males	821	46	21	33	0	<1	<1	0	<1
Females	1,491	46	22	31	0	<1	1	0	<1
Feeding									
Males	653	44	13	42	0	<1	<1	<1	<1
Females	921	51	10	38	<1	0	1	0	<1
<i>Colobus badius</i>									
Travel									
Males	1,194	35	31	29	0	0	3	0	2
Females	1,995	33	30	29	<1	0	3	0	4
Feeding									
Males	669	47	14	36	<1	0	2	0	1
Females	1,060	43	18	37	<1	0	2	0	<1
<i>Colobus guereza</i>									
Travel									
Males	751	39	44	11	<1	0	<1	0	6
Females	1,252	39	45	10	0	0	<1	0	5
Feeding									
Males	710	44	30	20	0	0	1	<1	5
Females	1,273	44	33	19	0	0	1	<1	3

<sup>1</sup> N = sample size. Other abbreviations as in Table 3.

TABLE 10. Use of positional behavior by sex and species across support sizes, support orientation, and canopy heights<sup>1</sup>

	Size				Angle				Canopy			
	N	L	M	S	N	H	O	V	N	U	M	L
<i>C. ascanius</i>												
Males	1,756	12%	53%	35%	1,756	53%	45%	2%	1,756	31%	58%	11%
Females	4,688	8	51	41	4,688	55	42	3	4,688	25	64	12
<i>C. mitis</i>												
Males	2,540	14	63	23	2,538	64	35	1	2,540	31	60	8
Females	3,901	13	60	28	3,885	61	39	1	3,901	34	60	6
<i>C. albigena</i>												
Males	2,299	17	60	23	2,288	56	40	4	2,287	31	61	8
Females	3,822	21	53	26	3,810	57	38	5	3,833	44	50	5
<i>C. badius</i>												
Males	2,855	20	67	13	2,856	49	48	3	2,860	50	42	8
Females	4,617	9	68	22	4,612	45	51	5	4,623	38	46	16
<i>C. guereza</i>												
Males	2,346	28	58	14	2,308	50	46	4	2,381	62	37	1
Females	3,623	20	62	17	3,509	46	51	3	3,873	60	37	3

<sup>1</sup> N = number of observations; L = large support; M = medium-sized support; S = small support; H = horizontal support; O = oblique support; V = vertical support; L = lower canopy, 0-5 m; M = middle canopy, 6-15 m; U = upper canopy, 16-25+ m.

saker, 1978). Its dietary overlap with the other Kibale Forest species is very low (Struhsaker, 1978).

*Colobus guereza*, the black and white colobus, is a frequent leaper (38%) and quadruped (41%) (Table 11). When leaping, *C.*

TABLE 11. Locomotor and postural frequencies<sup>1</sup>

	Locomotor frequencies (travel and feeding combined)								
	Bouts	Q	L	CL	QS	BR	BM	BI	VB
<i>Cercopithecus ascanius</i>	3,653	39%	15%	43%	0%	<1%	<1%	0%	3%
<i>Cercopithecus mitis</i>	3,413	54	11	35	<1	<1	<1	0	<1
<i>Cercocebus albigena</i>	3,911	47	17	35	<1	<1	1	<1	<1
<i>Colobus badius</i>	4,949	37	25	32	<1	0	3	<1	2
<i>Colobus guereza</i>	4,143	41	38	15	<1	0	1	<1	5

	Locomotor frequencies by equal weighting (travel % + feeding %)/2								
	Bouts	Q	L	CL	QS	BR	BM	BI	VB
<i>Cercopithecus ascanius</i>	3,653	40%	18%	38%	0%	1%	<1%	0%	4%
<i>Cercopithecus mitis</i>	3,413	53	12	33	<1	<1	<1	0	1
<i>Cercocebus albigena</i>	3,911	46	12	36	<1	<1	<1	<1	<1
<i>Colobus badius</i>	4,949	39	24	33	1	0	3	0	2
<i>Colobus guereza</i>	4,143	43	38	15	<1	0	1	<1	5

	Postural frequencies (travel and feeding combined)								
	Bouts	S	ST	RC	VCL	QSU	HSU	SBM	BIP
<i>Cercopithecus ascanius</i>	2,797	70%	26%	<1%	<1%	0%	<1%	0%	4%
<i>Cercopithecus mitis</i>	3,031	64	32	2	<1	<1	0	0	3
<i>Cercocebus albigena</i>	2,254	66	30	3	1	<1	<1	<1	1
<i>Colobus badius</i>	2,566	90	8	1	<1	<1	0	<1	1
<i>Colobus guereza</i>	2,309	87	4	8	<1	0	0	<1	<1

<sup>1</sup> Q = quadrupedalism; L = leaping; CL = climbing; QS = quadrupedal suspensory movements; BR = bridging; BM = bimanualism; BI = bipedalism; VB = vertical bounding; S = sitting; ST = standing; RC = reclining; VCL = vertical clinging; QSU = quadrupedal suspension; HSU = hindlimb suspension; SBM = bimanual suspension; BIP = bipedal stand. In equal weighting, locomotor percentages during travel and feeding are averaged rather than being combined as in total locomotor frequencies. Few differences are detected but note that climbing and leaping decrease by 5% respectively in *C. ascanius* and for *C. albigena*. This indicates that these locomotor activities are over represented in travel or feeding relative to each other (see Table 6).

*guereza* uses horizontal to horizontal supports frequently (Table 4). Bounding up vertical supports, as well as bounding and galloping along horizontal, usually large diameter supports, is also commonly observed in the black and white colobus (see also Morbeck, 1975, 1977, 1979; Mittermeier and Fleagle, 1976; and Rose, 1979). *C. guereza* prefers the upper canopy, horizontal and oblique supports, and medium-sized supports (Table 12). Although our height data (Table 12) shows a preference for the upper canopy for *C. guereza*, this may be an artifact since black and white colobus monkeys were more wary of observers than were the other monkeys (see Struhsaker and Oates, 1975; Struhsaker, 1978; Morbeck, 1977; Rose, 1978, 1979). At rest ( $n = 804$ ), *C. guereza* prefers to sit (78%), to stand (1%), and to recline (21%). *C. guereza*'s folivorous diet is very monotonous due to a particular use of a single tree species, *Celtis durandii*, and the heavy consumption of mature leaves of this species (Struhsaker and Oates, 1975; Struhsaker, 1978).

Comparing our study of *C. guereza* with others shows many similarities (Morbeck, 1975, 1976, 1977, 1979; Mittermeier and Fleagle, 1976; Rose, 1978, 1979). All studies have noted black and white colobus's tendency to gallop or to bound across horizontal supports (Morbeck, 1975, 1977, 1979; Mittermeier and Fleagle, 1976; Rose, 1979). These studies describe several types of leaps (i.e., from a standing position or from a running start; pumping a branch up and down, or simply dropping downward), and note that leaps are common. Rose (1978) notes that horizontal to horizontal or oblique to oblique leaps are the most frequent (Table 4). Leaps also tend to be fairly short in distance (2-6 feet; Morbeck, 1975, 1977; Tables 4 and 5). Further, all studies have documented that quadrupedalism and leaping are the two most common types of locomotor behavior (Morbeck, 1975, 1976, 1977, 1979; Mittermeier and Fleagle, 1976; Rose, 1978, 1979). On the other hand, Rose (1978, 1979) noted a higher use of climbing than these other studies, including our own. Fur-

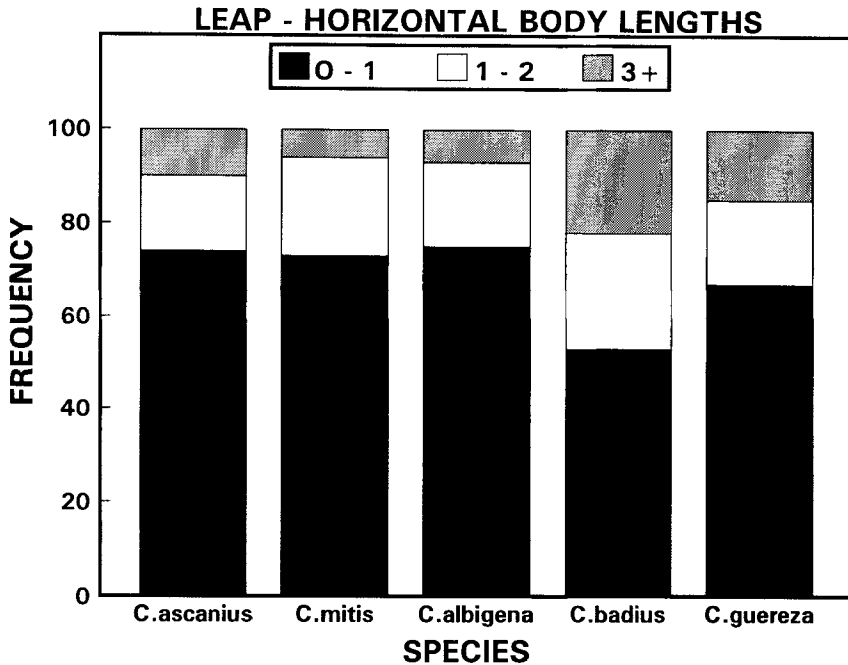


Fig. 2. Horizontal or linear distance crossed during a leap and measured in body lengths for all five species.

TABLE 12. Positional behavior relative to support size, orientation, and canopy height<sup>1</sup>

	Size				Angles				Canopy			
	N	L	M	S	N	H	O	V	N	U	M	L
All positional behavior												
<i>C. ascanius</i>	6,444	9%	52%	39%	6,444	55%	43%	2%	6,444	26%	62%	11%
<i>C. mitis</i>	6,441	13	61	26	6,423	61	38	1	6,441	33	60	7
<i>C. albigena</i>	6,121	20	55	25	6,098	57	39	5	6,120	39	54	6
<i>C. badius</i>	7,472	14	68	19	7,468	46	50	4	7,483	42	45	13
<i>C. guereza</i>	5,969	23	61	16	5,816	48	49	3	6,254	61	37	2
Only locomotion												
<i>C. ascanius</i>	3,648	10%	53%	37%	3,648	52%	44%	4%	3,537	26%	63%	11%
<i>C. mitis</i>	3,413	14	62	24	3,399	59	39	2	3,364	31	61	7
<i>C. albigena</i>	3,882	18	57	25	3,859	52	41	7	3,864	44	50	5
<i>C. badius</i>	4,911	14	68	18	4,917	42	52	6	4,688	42	45	13
<i>C. guereza</i>	3,772	22	62	16	3,662	46	50	4	3,995	58	40	2
Only postures												
<i>C. ascanius</i>	2,795	8%	50%	42%	2,796	58%	41%	1%	2,795	27%	61%	11%
<i>C. mitis</i>	3,029	13	59	28	3,024	63	37	<1	3,027	35	59	7
<i>C. albigena</i>	2,239	22	53	25	2,239	64	34	2	2,234	39	55	5
<i>C. badius</i>	2,561	13	67	20	2,551	52	47	1	2,553	44	44	12
<i>C. guereza</i>	2,197	25	59	16	2,154	52	45	2	2,247	66	33	1

<sup>1</sup>N = number of observations; L = large support (more than 25 cm in circumference); M = medium-sized support (between 6 and 25 cm in circumference); and S = small support (<5 cm in circumference); H = horizontal supports; O = oblique supports; and V = vertical supports; vertical height zones (L = 0-5 m; M = 6-15 m; U = 16-25+ m).

ther, quadrupedalism, although primarily used on medium-sized supports, often occurred on larger supports (Morbeck, 1977; Table 13). Likewise, bimanual pull-ups are

commonly observed after leaps (Morbeck, 1977). Mittermeier and Fleagle (1976), Morbeck (1979), and Rose (1979) all note that *C. guereza* prefers to sit during feeding and

TABLE 13. Support size, orientation, and locational use for each specific type of positional behavior<sup>1</sup>

	Canopy				Angle				Size			
	N	U	M	L	N	H	O	V	N	L	M	S
<i>Cercopithecus ascanius</i>												
Q	1,421	24%	64%	12%	1,421	64%	36%	0%	1,421	12%	64%	24%
L	548	20	70	11	548	46	52	2	548	9	63	28
CL	1,560	30	60	10	1,560	46	51	3	1,560	4	42	54
QS	0	0	0	0	0	0	0	0	0	0	0	0
BR	22	32	50	18	20	55	40	5	20	0	55	45
BM	8	0	88	12	8	25	75	0	8	0	63	37
BI	0	0	0	0	0	0	0	0	0	0	0	0
VB	91	29	47	24	91	0	11	89	91	90	10	0
S	1,945	27%	62%	11%	1,945	57%	42%	<1%	1,945	8%	51%	41%
VCL	5	0	60	40	5	20	20	60	5	60	20	20
QSU	0	0	0	0	0	0	0	0	0	0	0	0
SBM	2	0	50	50	2	50	50	0	2	0	50	50
HSU	0	0	0	0	0	0	0	0	0	0	0	0
ST	718	29	60	11	718	61	38	1	718	6	48	46
BIP	125	29	58	14	125	61	38	1	125	3	54	44
RC	1	100	0	0	1	0	100	0	1	0	0	100
<i>Cercopithecus mitis</i>												
Q	1,833	37%	57%	6%	1,828	80%	21%	0%	1,833%	15%	64%	21%
L	360	19	72	9	357	64	35	1	360	10	75	15
CL	1,178	26	65	9	1,173	28	69	3	1,178	11	57	31
QS	1	0	100	0	1	0	100	0	1	0	0	100
BR	12	33	50	17	12	42	58	0	12	0	33	67
BM	8	50	50	0	8	75	25	0	8	0	63	37
BI	0	0	0	0	0	0	0	0	0	0	0	0
VB	20	0	100	0	20	0	30	70	20	85	15	0
S	1,935	35%	58%	7%	1,931	61%	39%	<1%	1,935	13%	60%	28%
VCL	1	0	100	0	1	0	0	100	1	100	0	0
QSU	2	0	100	0	2	50	50	0	2	0	0	100
SBM	0	0	0	0	0	0	0	0	0	0	0	0
HSU	0	0	0	0	0	0	0	0	0	0	0	0
ST	955	35	59	6	954	66	34	<1	955	14	57	29
BIP	78	23	68	9	78	62	38	0	78	12	64	24
RC	58	31	64	5	58	66	33	2	58	22	69	9
<i>Cercopithecus albigena</i>												
Q	1,813	43%	52%	5%	1,807	70%	30%	0%	1,815%	23%	58%	19%
L	675	40	52	8	659	57	39	4	671	16	64	20
CL	1,352	34	58	9	1,341	27	58	15	1,370	12	52	35
QS	1	0	0	100	1	100	0	0	1	0	0	100
BR	10	10	80	10	10	40	60	0	10	0	30	70
BM	24	29	63	8	24	21	79	0	24	0	29	71
BI	2	100	0	0	2	100	0	0	2	0	100	0
VB	9	56	44	0	9	0	11	88	9	89	11	0
S	1,473	39%	54%	7%	1,474	64%	35%	1%	1,471	18%	58%	24%
VCL	13	8	69	23	13	0	15	85	13	46	31	23
QSU	2	50	50	0	2	0	100	0	2	0	0	100
SBM	3	67	33	0	3	100	0	0	3	0	67	33
HSU	1	0	100	0	1	100	0	0	1	0	100	0
ST	657	40	57	3	659	65	34	1	661	25	47	28
BIP	29	24	76	0	29	55	45	0	29	17	28	55
RC	55	65	35	0	58	79	21	0	58	76	21	2
<i>Colobus badius</i>												
Q	1,862	46%	43%	11%	1,861%	62%	38%	0%	1,861	15%	71%	14%
L	1,254	39	46	16	1,246	44	54	2	1,249	11	73	16
CL	1,573	39	47	15	1,570	24	66	10	1,569	13	63	24
QS	5	60	40	0	5	20	80	0	5	0	40	60
BR	0	0	0	0	0	0	0	0	0	0	0	0
BM	125	32	52	16	125	29	72	0	125	6	61	33
BI	1	0	100	0	1	100	0	0	1	0	100	0
VB	109	31	50	19	109	0	26	73	109	63	35	2
S	2,297	45%	43%	12%	2,294	52%	48%	1%	2,296	13%	68%	20%
VCL	8	25	75	0	8	0	0	100	8	25	50	25
QSU	1	0	100	0	1	100	0	0	1	0	100	0
SBM	5	100	0	0	5	40	60	0	5	0	80	20

(continued)

TABLE 13. Support size, orientation, and locational use for each specific type of positional behavior<sup>1</sup> (continued)

	Canopy				Angle				Size			
	N	U	M	L	N	H	O	V	N	L	M	S
<i>Colobus badius</i> (continued)												
HSU	0	0	0	0	0	0	0	0	0	0	0	0
ST	203	39	52	9	203	66	34	0	203	12	67	22
BIP	20	60	35	5	20	45	55	0	20	20	40	40
RC	19	47	37	16	19	32	68	0	19	16	68	16
<i>Colobus guereza</i>												
Q	1,653	61%	38%	1%	1,542	60%	40%	0%	1,582	26%	60%	14%
L	1,517	55	44	2	1,330	49	49	2	1,365	19	70	13
CL	597	61	36	3	582	12	80	9	590	18	52	31
QS	1	100	0	0	1	0	100	0	1	0	0	100
BR	0	0	0	0	0	0	0	0	0	0	0	0
BM	28	67	34	1	26	38	62	0	27	4	63	33
BI	2	0	100	0	2	0	100	0	2	0	100	0
VB	197	44	45	11	179	12	52	36	187	34	61	4
S	1,944	65%	34%	1%	1,864	51%	48%	1%	1,899	24%	59%	2%
VCL	10	40	60	0	8	0	0	100	10	60	40	0
QSU	3	100	0	0	2	50	50	0	1	100	0	0
SBM	2	50	50	0	0	0	0	0	2	0	100	0
HSU	0	0	0	0	0	0	0	0	0	0	0	0
ST	102	76	23	1	94	62	36	2	98	24	53	22
BIP	3	33	67	0	3	33	67	0	3	33	67	0
RC	185	69	31	0	183	61	39	0	184	32	60	8

<sup>1</sup>Abbreviations as in Table 3.

rest periods, although reclining was fairly frequent (Table 6). Morbeck (1977) and Rose (1978, 1979) note that black and white colobus preferred the middle canopy, although our data shows an upper canopy bias (Table 12). Rose (1979) also documents that *C. guereza* prefers to rest on horizontal supports and that horizontal and oblique supports are used about equally often during movements (Table 12). Morbeck (1977) and Rose (1978) further record that black and white colobus monkeys prefer medium-sized supports (Table 12).

## SPECIES COMPARISONS

### Locomotion

Comparing the two guenons shows that *C. ascanius* leaps and climbs more often than *C. mitis*, while *C. mitis* prefers quadrupedalism; these differences are statistically significant (Tables 8 and 11). *C. ascanius* also uses climbing and leaping more often during feeding than *C. mitis* (Table 6), and vertically bounds up tree trunks in all canopy heights (Table 13). Although the smallest of the five species studied at Kibale Forest, *C. ascanius* leaps only slightly more than *C. mitis*, and slightly less than the much larger *C. albigena* (statistically significant, Table 8). In

contrast to *C. ascanius*, *C. mitis* is a far heavier user of quadrupedalism (Tables 8 and 11).

Although *C. albigena* is the largest of the three cercopithecines, it possesses the highest leaping frequency. *C. albigena* also vertically climbs more often than the other cercopithecines (Table 13). Relative to the similarsized colobines, *C. albigena* uses quadrupedalism more, and leaping, climbing, bimanualism, and bounding less often (Table 11). *C. albigena* shows statistically significant differences in leaping compared to both colobines, and is statistically different from *C. badius* and *C. guereza* in frequencies for quadrupedalism and climbing, respectively (Table 8). Horizontal distances crossed while leaping, as well as vertical distances downward, are similar in all three cercopithecines, but in colobines these distances are longer (Table 4).

*C. badius* leaps more often than any of the cercopithecines, but less often than *C. guereza*; these differences are statistically significant (Tables 8 and 11). It also uses bimanualism more than any other species, and climbs less than any cercopithecine (Table 11). Compared to *C. guereza*, the horizontal distance covered during a leap in red colobus monkeys is greater, as is the vertical

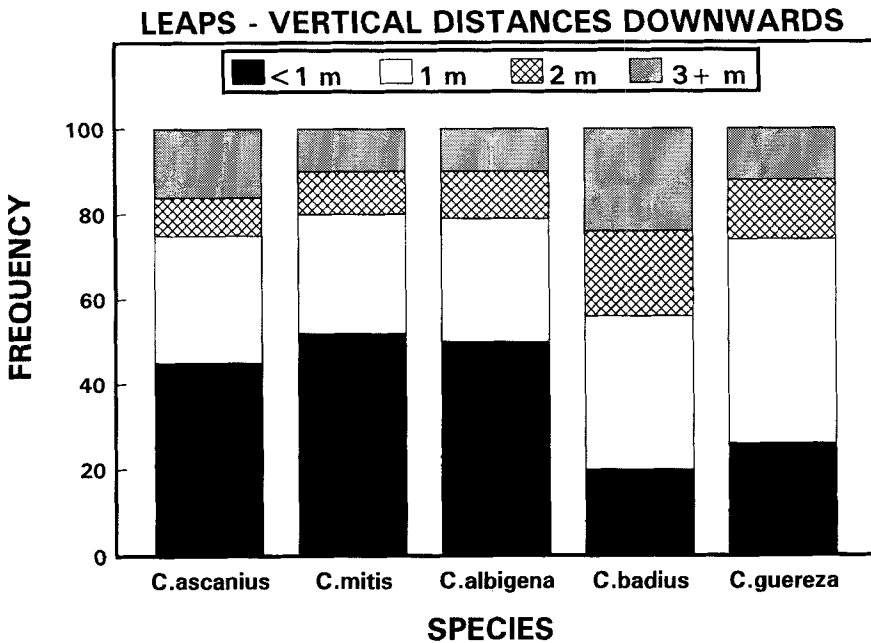


Fig. 3. Vertical descent during a leap measured in body lengths for all five species.

drop (Fig. 3). As with the cercopithecines, *C. guereza* tends to leap over short distances, staying within a fairly horizontal pathway (Fig. 4). This is in stark contrast to the out and downward descent of red colobus leaps (see below). *C. guereza*'s use of vertical bounding, leaping, and climbing differs statistically from that of the other four species (Table 8). Both colobines, although large-sized, leap more often and cover longer horizontal distances than do the cercopithecines. Vertical climbing is also more frequently observed in both colobines than in the guenons. Bridging was not observed in the colobines.

When red colobus monkeys leap, they tend to leap outward and drop large distances downward (Table 4; Figs. 3 and 4). Struhsaker (1975, p. 4) notes vertical drops between 5 and 10 m and describes red colobus locomotion as being best "described as suicidal." Like most anthropoids, red colobus starts the air phase part of its leap with a horizontally positioned body and arms and legs spread-eagled. As an individual drops, the body reorients into a more vertical position with the legs spread, the feet oriented

toward the ground, and the arms raised above the head (Fig. 4). This is the usual body position when red colobus lands, with its feet hitting a branch first. It then attempts to grasp onto a branch with its feet (often slipping off and only braking or slowing its falling body), while the hands and arms act as hooks on branches above the head to stop the downward descent as the individual impacts the now shaking and waving branches. This vertical body orientation during landing forces red colobus monkeys to use bimanual pull-ups more frequently (Table 8) and to use vertical/oblique support climbing sequences on small diameter supports often. See Ripley (1967, p. 161) for a similar description of leaping in langurs.

### Postures

The frequency of sitting and standing postures are similar in red-tailed and blue monkeys; both guenons utilize bipedal standing quite often during feeding compared to the other species (Tables 6 and 8). *C. ascanius* rarely reclines relative to *C. mitis*. Like the guenons, *C. albigena* uses standing more of-



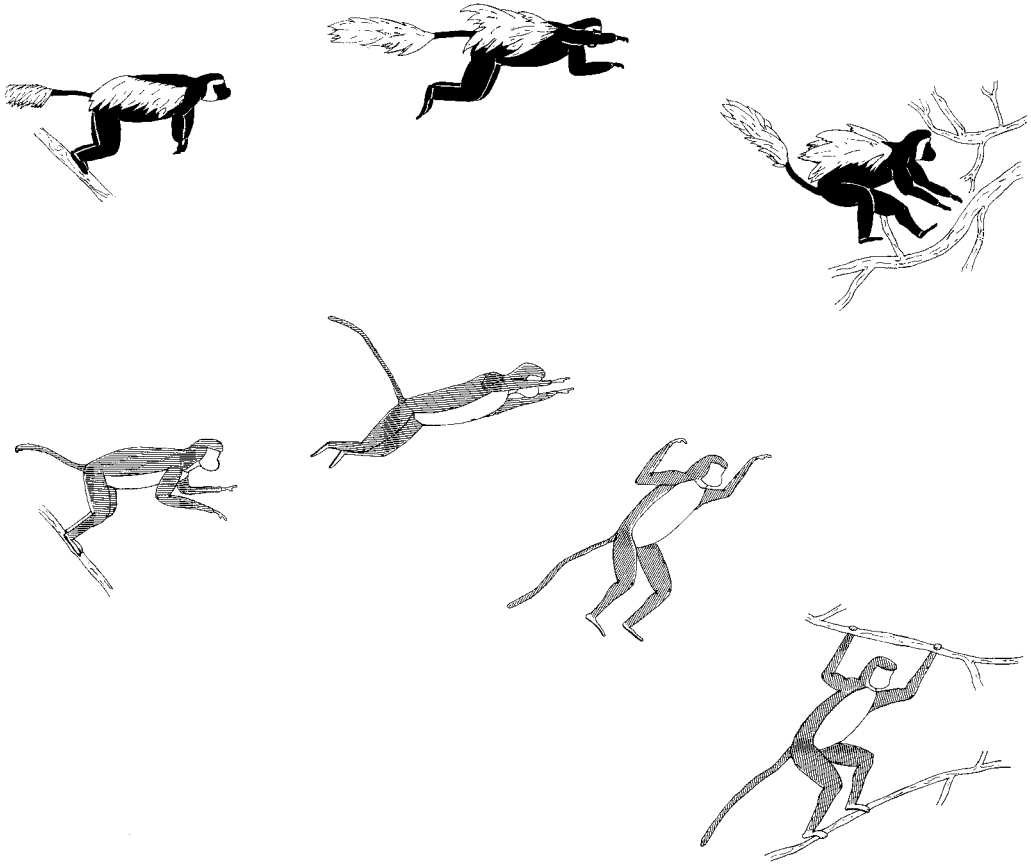


Fig. 4. Leaping postures in *C. guereza* (top) and *C. badius* (bottom). Note the vertical body orientation and the greater vertical descent in the leaps of red colobus monkeys.

ten than the colobines (Table 8). Both colobines tend to sit more, and stand less (Table 8) than the cercopithecines. Note the larger frequency for reclining in *C. guereza* (8%), compared to *C. badius* (1%) (Tables 8 and 11).

### Support sizes

All five species, regardless of body size, use medium-sized supports (6–25 cm in circumference) approximately half to two-thirds of the time (Table 12). Examining support use on large or small supports however does exhibit a better gradient of use according to size. *C. ascanius*, the smallest species, utilizes the smallest supports (<5

cm in circumference) most often, while *C. guereza*, the largest species, utilizes the largest supports most frequently. *C. mitis*, the larger of the two guenons, uses larger supports (medium and large) more often than the smaller *C. ascanius*. Likewise, the largest colobine, *C. guereza*, uses large diameter supports more often than the smaller *C. badius*. On the other hand, *C. albigena*, a smaller-sized monkey relative to the colobines, uses large diameter supports more often than the larger *C. badius*.

Table 13 separates each specific type of positional behavior in context to its support use size and further documents the complexity of support size usage and body size differences. For example, bridging usually occurs

on small-sized supports in *C. mitis* but the smaller *C. ascanius* uses medium-sized supports more often for this movement. *C. albigena* uses bimanualism on smaller supports while the guenons and colobines prefer medium-sized supports. Further, *C. guereza* bounds up medium-sized supports, while the smaller *C. badius* bounds up large-sized supports more often. Therefore, even single movement comparisons relative to support sizes do not always provide consistent trends according to body size.

### Support angles

All five species use all types of supports (horizontal, oblique, and vertical), with vertical supports being utilized least often (Table 12). The three largest species, *C. albigena*, *C. badius*, and *C. guereza*, use vertical supports more often than the smaller guenons. The three cercopithecines prefer horizontally oriented supports, while the colobines use horizontal and oblique supports about equally often, with oblique supports being used slightly more frequently. Both colobines prefer to use horizontal supports more often during postural activities, and oblique supports during locomotor activities (Tables 12 and 13). For all five species, higher frequencies of horizontal support use are recorded during postures as compared to locomotion. Vertical supports are rarely utilized for postures (Tables 12 and 13).

### Leaping from/to supports

In all species, leaping from horizontal to horizontal and oblique to oblique supports occurred most frequently (Table 4). Horizontal to oblique or oblique to horizontal leaps make up virtually all the rest. As expected, leaps from or to vertical supports are rare. For the cercopithecines, *C. ascanius* leaps using horizontal to horizontal supports and oblique to oblique supports about equally often. In contrast, *C. mitis* and *C. albigena* exhibit a horizontal to horizontal preference. Both colobines are similar in their use of horizontal to horizontal and oblique to oblique leaps, with *C. guereza* using horizontal to horizontal leaps more relative to *C. badius* (Table 4). During leaping, the larger *C.*

*badius* has a similar pattern of support use as does the smaller *C. ascanius* (Table 4).

### Canopy height

All five species use each of the three height zones (upper, middle, and lower) within the canopy (Table 12). Four species prefer the middle zone, with only *C. guereza* preferring the upper heights most often. *C. badius*, and to a lesser extent *C. albigena*, utilize the upper and middle zones about equally often. The guenons clearly prefer the mid-canopy over the upper canopy. Both *C. ascanius* and *C. badius* utilize the lowest height zone more frequently than the other three species. *Colobus guereza* rarely uses the lower canopy. Table 13 provides a more detailed examination of where each type of positional behavior is performed within the canopy height zones by species. For example, sitting, standing, reclining, and bimanualism are often observed in the upper canopy in *C. guereza*, while these postures are more evenly distributed in the upper and mid-canopy in *C. badius*. All five species were observed to come to the ground occasionally.

### Tree use

Based on scanning the spatial position of individuals at 10 minute intervals, it is evident that the crown of the tree is used much more than are the major branches or the trunk of a tree, with two exceptions (Table 7). *C. albigena* uses the crown only slightly more often than the major branches and thus uses both aspects of tree structure more equally when compared to the other species. *C. guereza* is very different in its use of tree structure with a decided preference for major branches. As expected, use of the trunk is rare for all of these Old World monkeys.

The data from the two 600 m transects, where distances between branches of adjacent trees (spatial gaps) were recorded, indicated that neighboring trees are in contact 42% of the time. Spatial gaps of 1 m or less represent 74% of the forest, while gaps of 2 m or less represent 90% of the forest. Thus, assuming that primates take the most direct route and that they do not attempt to travel around a gap, the study animals were faced

with long distances (over 2 m or in excess of four body lengths) between trees only 10% of the time.

Since bridging and terrestriality were very rarely observed, leaping represents the only frequently used movement for crossing these spatial gaps between trees. Thus, for *C. albigena*, with an average body length of 540 cm, a two body length leap represents about a 1 m gap and these monkeys should encounter a gap of this distance or less about 74% of the time when moving between trees. *C. albigena* makes leaps of two body lengths (about 1 m) or less 93% of the time (Table 4). This is also true for the other two cercopithecines. Spatial gaps of 2 m or more represent 10% of the primary forest area, and are very rarely tackled by leaping by *C. albigena* or by *C. mitis* (Table 4). *C. guereza* and *C. ascanius* will leap these longer distances slightly more often (about 5%), but only *C. badius* attempts these leaps more regularly (10%) (Table 4). If the distance of the gap is too large to leap across, an alternative route through the canopy is usually the choice of preference for all five species. The last choice is to cross via the ground—a choice more often observed in the black and white colobus than for the other four species.

If we combine the ten most common trees in Kibale Forest (Table 1), accounting for approximately 73% of the trees in the area, into a single hypothetical model tree, we arrive at a tree 21.4 m in height with a DBH of 38.4 cm, and a crown volume of 1,533 m<sup>3</sup>. This hypothetical tree will possess 8.4 medium-sized and 2.2 large-sized horizontal branches, 18 medium-sized and 4.4 large-sized oblique branches, and 1.6 medium-sized and 1.7 large-sized vertical supports (Table 1). This, at best, is a crude generalization; however, we believe it provides a useful heuristic tool to consider support use relative to availability. This model indicates that vertical supports are rare within the forest. Correspondingly, all five species of monkeys rarely use vertical supports, relative to their use of horizontal and oblique supports (Table 12). Oblique supports are the most common within the forest (Table 1) and colobines use these supports often (Table 12). However, the three cercopithecines use horizontal supports more frequently

(Table 12) and therefore are choosing less common supports for their movements. The most frequently used support size is the medium-sized branch (between 6 and 25 cm in circumference). Each species uses this size support over 50% of the time (Table 12). Large-sized supports (>25 cm in circumference) are utilized least often by all species with *C. guereza* possessing the highest usage, 23% (Table 12). The smallest monkey, *C. ascanius*, uses the smallest supports most often (39%), while the other species range in their use from 16 to 26% (Table 12). Of course, if the total number of branch sizes within the forest and in our hypothetical model tree included small branches, it is abundantly clear that these smaller supports would clearly outnumber their medium and large-sized counterparts by an order of magnitude. Thus, since none of our five monkey species are using these small-sized supports in accordance to their relative abundance, a choice is being made, a choice that likely coincides with the size of the monkey relative to the diameter of the support and the anatomical constraints of the species in question.

#### Activity (travel vs. feeding)

For all species, there are greater differences in locomotor frequencies during feeding than during travel (Table 6), and this is especially true across the sexes (Table 9). Quadrupedalism is similar (within 5%) across activities, with the exception of *C. badius* where quadrupedalism is 10% higher during feeding than for travel (Table 6). Leaping frequencies decrease uniformly (a 10% decrease or more in frequency) across all five species during feeding (movements within a single tree) compared to travel. Climbing frequencies increase for each of the five species during feeding (Table 6). Vertical bounding is more often observed during travel than during feeding for all species except *C. albigena*. Red-tailed monkeys use vertical bounding sequences more often during travel relative to the other species (Table 12).

For postures, sitting increases during feeding for two of the three cercopithecine species, with the exception being *C. ascanius*. For colobines, sitting increases slightly

TABLE 14. Locomotor behavior by activity and species relative to canopy use, support orientation, and support sizes<sup>1</sup>

	Canopy				Angles				Sizes			
	N	UC	MC	LC	N	H	O	V	N	L	M	S
<i>C. ascanius</i>												
Travel	1,125	13%	72%	15%	1,121	43%	47%	10%	1,128	16%	64%	20%
Feed	2,527	31	59	10	2,501	56	43	1	2,517	8	48	44
<i>C. mitis</i>												
Travel	1,367	24	67	8	1,356	58	39	3	1,367	17	70	13
Feed	2,016	36	57	7	2,011	60	39	1	2,035	11	57	32
<i>C. albigena</i>												
Travel	2,336	40	52	8	2,279	51	42	7	2,301	20	58	22
Feed	1,574	38	56	6	1,422	52	41	6	1,565	16	55	29
<i>C. badius</i>												
Travel	3,190	34	51	16	3,181	42	50	7	3,181	15	70	15
Feed	1,737	54	35	10	1,643	45	52	2	1,725	12	64	24
<i>C. guereza</i>												
Travel	2,003	50	46	4	1,790	48	47	6	1,882	27	60	13
Feed	1,983	66	33	1	1,361	46	51	3	1,910	17	64	19

<sup>1</sup>N = number of observations; UC = upper canopy; MC = middle canopy; LC = lower canopy; H = horizontal support; O = oblique support; V = vertical support; L = large support; M = medium-sized support; S = small support.

for *C. badius*, but decreases for *C. guereza* (Table 6). The frequencies for standing remain similar for both travel and feeding activities, with the exceptions of *C. mitis* and *C. albigena*, where standing is much higher during travel. In contrast, Rose (1974) records very high percentages for sitting and very low percentages for standing during feeding in *C. mitis* and *C. ascanius*. Bipedal standing increases in frequency for all five species during feeding (see Rose, 1976, for situations eliciting bipedalism). Other types of positional behavior comparisons in Table 6 are generally similar across activity.

The upper canopy is utilized most often for feeding by four of the five monkey species, with the exception being *C. albigena*, which feeds most often in the middle canopy. This indicates an upward directional choice in attaining food resources. The middle canopy is used most often during travel for all five species, with about equal use of the mid- and upper canopy by *C. albigena*. The lower canopy is utilized slightly more often for travel than for feeding (Table 14).

Vertical supports are rarely used during feeding; the highest frequency is *C. albigena*'s 6% (Table 14). Vertical supports are used more often during travel in all species. During travel, *C. ascanius* is an especially frequent user of vertical supports (Table 14). Oblique supports are utilized about evenly for both travel and feeding activities for all species. Horizontal supports are used about

equally (within 3%) across activities for four species, with *C. ascanius* using horizontal supports more often during feeding (Table 14).

All five species prefer smaller supports during feeding compared to travel (Table 14), while large diameter supports are used more often for travel. Guenons utilize medium-sized supports most often during travel while the three larger species prefer medium-sized supports equally often across activity (Table 14). *C. guereza* often uses large-sized supports while traveling.

### Movement distances

During travel, bout lengths of 4 or 4+ body lengths are more frequently recorded for quadrupedalism and climbing than at other times (Table 5; Fig. 5). During feeding, most distances are less than two body lengths (Fig. 5). Leaping is more equivocal, but the frequency of body lengths of two or greater does increase during travel. Therefore, during feeding, bouts of climbing and quadrupedalism generally cover shorter distances, while the reverse is true during travel.

Mean bout distances during travel are greater than mean bout distances during feeding for quadrupedalism, climbing, and leaping in all five species (Table 5). The distances for leaping are, however, more similar across activity. Mean distances for each movement type are very similar across spe-

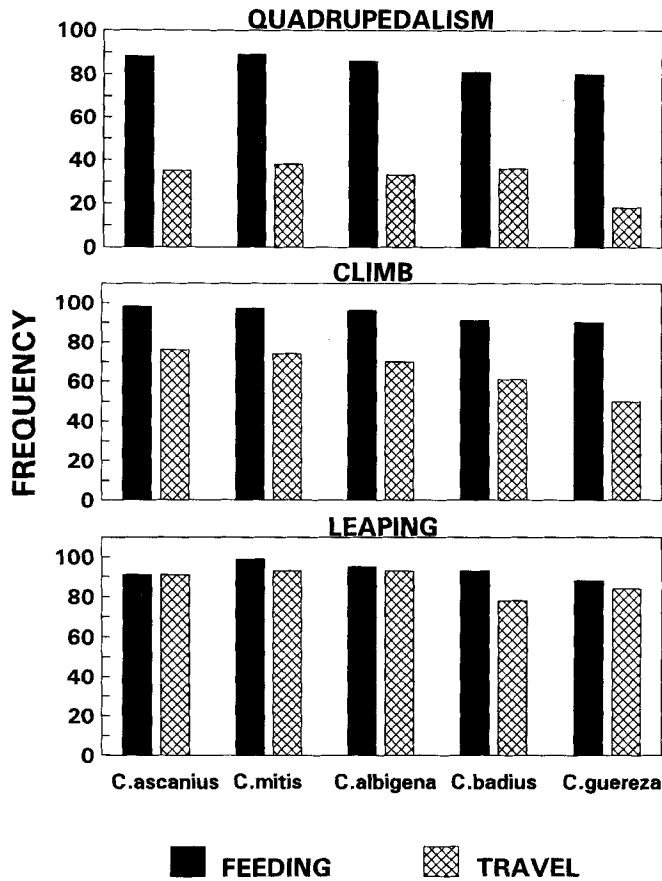


Fig. 5. Movement frequencies for quadrupedalism, climbing, and leaping during travel and feeding within distances of <1–2 body lengths (about 1 m) in linear distance for all five species.

cies. An especially high distance value for quadrupedalism during travel is recorded for *C. guereza*, and both colobines show higher mean distances for climbing during travel compared to cercopithecines.

Using Doran's (1992) conversion formula for locomotor frequencies over distance documents *C. ascanius* using about equal amounts of quadrupedalism and climbing during feeding, while *C. mitis* favors the use of quadrupedalism. Converted frequencies for *C. albigena* and *C. badius* show that both species move with a similar locomotor pattern during feeding, but differ during travel where quadrupedalism is emphasized in *C. albigena* and leaping in *C. badius* (Table 6).

In contrast, *C. guereza* often uses leaping while feeding compared to the other species.

Mean day ranges show that cercopithecines move about twice as far daily as do the two colobines (Table 2). However, mean day ranges differ very little between species relative to their respective subfamily (Table 2). Thus, differences in positional behavior, tree use, or body sizes across species do not appear to be related to changes in day range.

## DISCUSSION

### Comparisons with Surinam

Some similarities emerge from a comparison of Fleagle and Mittermeier's (1980)

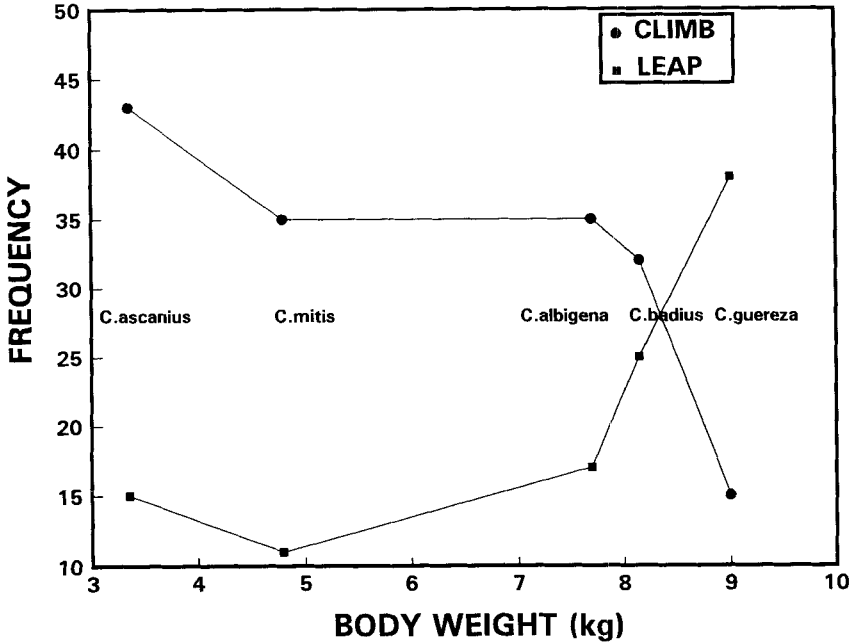


Fig. 6. Climbing and leaping frequencies by species and body weight. Note as size increases, the decrease in climbing frequencies and the increase in leaping frequencies.

study of seven sympatric New World monkeys with our study of five sympatric Old World monkeys. For example, Fleagle and Mittermeier (1980) found that during feeding (relative to travel) leaping frequencies are reduced, climbing frequencies increase, movement distances decrease, and the use of smaller supports increase in frequency. Our study also documented climbing increases and leaping decreases across all species and sexes during feeding. Likewise, both studies document that mean feeding distances are shorter for quadrupedalism, climbing, and leaping than they are for travel, although mean leaping distances in *C. ascanius* are almost identical, and mean leaping distances are generally similar across activity compared to quadrupedalism and climbing in cercopithecids. As with the platyrrhine data, the results from Kibale Forest demonstrate that smaller supports are utilized more often during feeding than during travel. Further, quadrupedalism did occur most often in the mid- and upper canopy levels in our Old World monkeys as it did in the Surinam platyrrhines.

On the other hand, many of the predictions of the Surinam study were not borne out by our study. For example, Fleagle and Mittermeier (1980) showed that leaping decreased and climbing increased as body size increased, with two exceptions (i.e., *Saguinus midas* and *Pithecia pithecia*). Our study shows just the opposite trend (Fig. 6). Figure 6 plots climbing and leaping frequencies across the mean body size of each of the five species from Kibale Forest. The larger Old World monkeys leap more often than do the smaller ones, while the reverse is true for climbing. The smallest species, *C. ascanius*, climbs most frequently and leaps rather infrequently compared to the others. Similarly, the largest species, *C. guereza*, leaps the most frequently and climbs least often. *C. mitis* climbs at approximately the same frequency as does the larger *C. albigena*.

If we divide climbing into two types, vertical climbing and the scrambling/clambering variety (see Cant, 1986, 1987b, 1988), all three of the larger species do utilize vertical climbing more often than do the two smaller

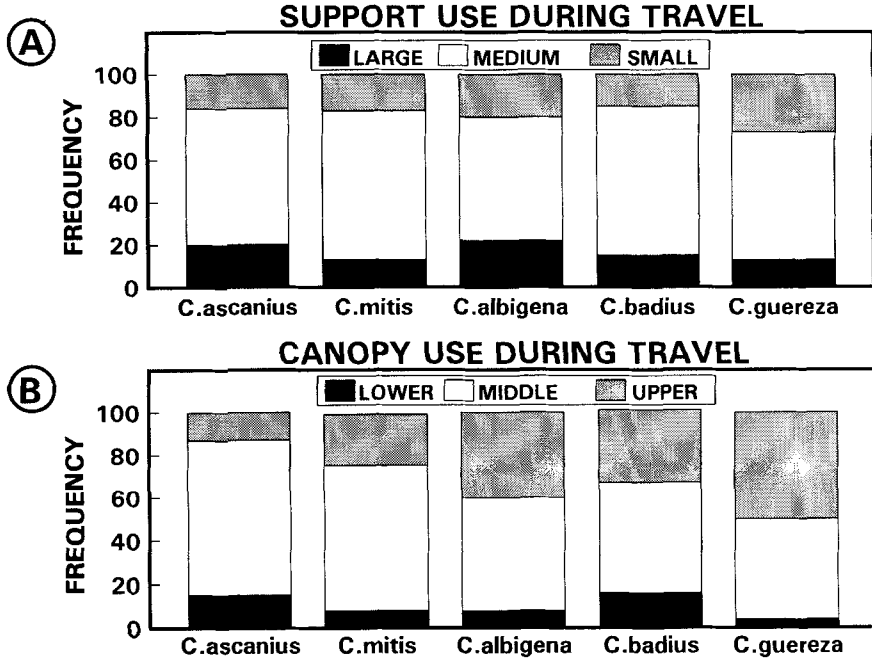


Fig. 7. Use of support sizes (A) and the canopy (B) during travel in order of a species' body weight. *C. ascanius* is the smallest in size while *C. guereza* is the largest.

guenons. *C. albigena* vertical climbs about 15% (5% of total locomotor bouts), the colobines about 10% (3% of total locomotor bouts), and the guenons about 3% (1% of total locomotor bouts) of their climbing bouts (Table 13). Again, the trend does not sort by body size alone (e.g., the largest species, *C. guereza*, is not the most frequent user of vertical climbing, nor is this species' value very different from the smaller *C. badius*).

Both colobines leap more frequently than do the more similar-sized *C. albigena*, which leaps as much as the smaller *C. ascanius*. Comparing only the cercopithecines also shows no clear trend in leaping frequencies relative to body size. For these five species of Old World monkeys, it appears that changes in body size do not correspond closely to changes in locomotor frequency. The tendency in these Old World monkeys is for body size increases to correspond to decreases in climbing and increases in leaping frequencies. Thus, changes in body size among different taxonomic groups of pri-

mates may well yield different associations between size and locomotor frequencies.

In platyrrhines, an increase in body size was associated with increased use of larger support sizes, especially for quadrupedal species, with *Saguinus midas* and *Ateles paniscus* noted as exceptions (Fleagle and Mittermeier, 1980). Fleagle and Mittermeier (1980, p. 310) stated that a "tight correlation between mass and size of supports used in quadrupedal walking and running" existed. Our study shows a more complex relationship between support sizes and body size in a group of monkeys with an admittedly more restricted range in body size. Figure 7 shows the use of different sized supports. Here, the third largest monkey, *C. albigena*, is the most frequent user of the smallest support sizes, while both *C. mitis* and *C. badius* most often use medium-sized supports.

In platyrrhines, leaping tends to occur most often in the understory and lower canopy where the forest is more discontinuous, while quadrupedalism and suspensory behavior occur more frequently in the middle

to upper canopy (Fleagle and Mittermeier, 1980). In contrast, our study demonstrates that leaping occurs most often in the mid- and upper canopy for each of the five species. Further, in our own study, we could only find a slight tendency for our smaller-sized species to use the lower canopy more (Fig. 7), but see *C. badius*. Thus, although points of agreement exist between these two multispecies studies on two different continents, the counter examples are problematical and highlight the need for future work.

### Comparisons with Asian Cercopithecids

Positional studies on Asian cercopithecids (e.g., *Presbytis entellus*, *P. vetulus*, *P. melalophos*, *P. obscura*, *Macaca fascicularis*, *M. sinica*, and *M. nemestrina*) describe similar patterns of positional behavior to our study of African monkeys. Both Asian and African cercopithecids emphasize quadrupedalism, leaping, climbing, sitting, and standing (Ripley, 1967; Rodman, 1979; Fleagle, 1980; Cant, 1988). All of these species would be categorized as arboreal quadrupeds, with perhaps the exception of *M. nemestrina*, a more terrestrial monkey. Several studies of these species have reported quantitative data so we can test for trends relating positional behavior to body size and morphology (i.e., intermembral index). All of these African and Asian cercopithecids are medium-sized monkeys ranging from mean body sizes of 3,585 g to 9,070 g, a 2.5 increase by weight (Table 15). The moderate size range and their generally similar postcranial anatomy also help to eliminate potentially conflicting variables.

Figure 8 makes three comparisons: body size with leaping frequency, body size with intermembral index, and leaping frequency with intermembral index. As Figure 8 shows, body size is not highly correlated with leaping frequency, nor is the correlation coefficient significantly different from zero ( $r = 0.534$ ,  $P = 0.138$ ). Thus, body size is a poor indicator of how often these species leap during travel. For example, among colobines, a small species (*P. obscura*) leaps less often than the largest species (*C. guereza*). Among cercopithecines, the leaping frequencies of the smallest (*C. ascanius*) and the largest (*C. albigena*) are almost the

TABLE 15. African and Asian cercopithecids<sup>1</sup>

	Body size	Leaping (%)	Intermembral index
Colobines			
Asian			
<i>P. melalophos</i>	6,648	67.5	78
<i>P. obscura</i>	6,810	40.2	83
African			
<i>C. badius</i>	8,245	30.0	87
<i>C. guereza</i>	9,070	44.0	79
Cercopithecines			
Asian			
<i>M. fascicularis</i>	4,030	11.0	93
African			
<i>C. ascanius</i>	3,585	25.0	79
<i>C. aethiops</i>	4,365	10.0	83
<i>C. mitis</i>	4,750	18.0	82
<i>C. albigena</i>	7,690	21.0	78

<sup>1</sup>Leaping frequencies during travel are from Rose (1979), Fleagle (1980), Cant (1988), and this manuscript. The values for *C. aethiops* and *M. fascicularis* are approximate. Mean body sizes in grams are from this manuscript and Fleagle (1988). Intermembral indices are from Fleagle (1988).

same. All four colobines leap more often than the cercopithecines, regardless of body size.

A low correlation also exists between intermembral index and body size (Fig. 8). Again, the correlation coefficient is not significantly different from zero ( $r = -0.291$ ,  $P = 0.448$ ). Despite a large range of body size, there is little difference in intermembral index. Further, vertical climbing is very rare in these cercopithecids and thus changes in intermembral indices are unlikely to be size-related due to functional competence for vertical climbing as noted by Jungers (1985).

Lastly, examining leaping frequency relative to the intermembral index shows a low correlation for these nine cercopithecids as well, and a correlation coefficient that is not significantly different from zero ( $r = -0.0491$ ,  $P = 0.180$ ; Fig. 8). Monkeys with vast differences in leaping frequency have the same or a similar intermembral index. For example, *C. ascanius*, *C. albigena*, *C. guereza*, and *P. melalophos* each possess an intermembral index of either 78 or 79, and yet the leaping frequencies vary from a low 21% to a high of 67.5%.

### CONCLUSIONS

Positional behavior and habitat use of five sympatric species of Old World monkeys living within Kibale Forest, Uganda, were ex-



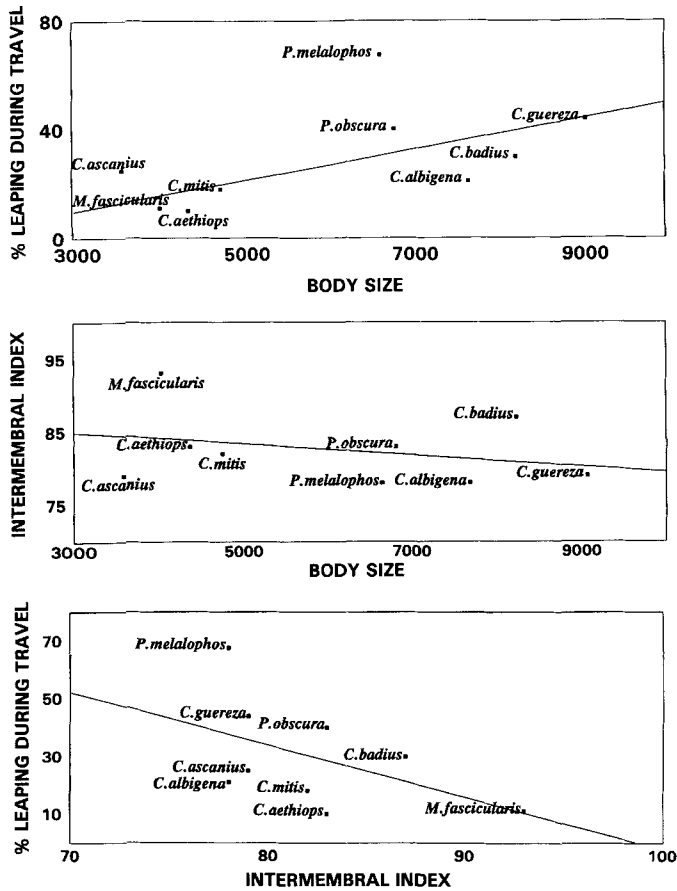


Fig. 8. Body size, leaping frequency during travel, and intermembral index comparisons across cercopithecids. Species values are listed in Table 15. Note the low correlation coefficient ( $r$ ) in each of these three comparisons (% leaping during travel vs. body size  $r = 0.534$ ,  $P = 0.138$ ; intermembral index vs. body size  $r = -0.291$ ,  $P = 0.448$ ; % leaping during travel vs. intermembral index  $r = -0.491$ ,  $P = 0.180$ ).

amined to identify the distinctive positional features of each species and to test relationships between behavior, body size, and habitat use. Being sympatric and closely related minimized the extraneous effects of differing habitats or alternative anatomies and limb function. All five species commonly utilize three varieties of locomotion (quadrupedalism, leaping, and climbing) and two postures (sitting and standing), and would likely be categorized as arboreal quadrupeds (see Rose, 1973). This categorization, however, obscures the climbing emphasis of the cercopithecines; the leaping tendency of *Colobus guereza*; and the more egalitarian use of climbing, leaping, and quadrupedal-

ism by the red colobus monkey. Each species is capable of performing all of the positional behaviors studied, from the common to the rarely observed varieties (e.g., bimanualism or vertical clinging). No single species utilized any of the rarer varieties of positional behavior in unusual frequencies, nor in special situations relative to that of the other species. Thus for these five species, choices were being made given their generally similar anatomical make-up, body size, and the structure of the habitat. How and why species make these behavioral choices is the driving question of current positional behavioral studies (see Avis, 1962; Prost and Sussman, 1969; Dykyj, 1980; Menzel, 1986; and

Roberts and Cunningham, 1986, for experimental studies on this issue).

In 1992, John Cant wrote a paper which offered a framework for research of positional behavior, body size, and habitat use, and emphasized the importance of the animal-habitat relationship (see also Napier, 1967; Cartmill, 1974, 1985; Charles-Dominique, 1977; Grand, 1984; Fleagle, 1985; Garber, 1980, 1992; Rodman, 1991; and Doran, 1993). Cant (1992) identified six problems that primates need to solve within the arboreal environment and proposed some research directions that might reveal the relative effectiveness of these solutions. This study, for example, examined the problem of crossing gaps, the structure of the habitat, and the inter- and intraspecific effects of body size on positional behavior within Cant's framework. After all of this work, we unfortunately must agree with Cant (1992, p. 282) when he states "we presently have only the most rudimentary understanding of how positional diversity might influence coexistence of sympatric species." Clearly, we have a lot more work to do. To obtain any generalized relationship between positional behavior and body size across a wide array of primate species will require far greater and more varied sampling before any generalizations may be forthcoming. Like Fleagle and Mittermeier's (1980) study, our study has added some data and insights into how species move within their habitat. One can only hope that in the future well-designed field studies will be able to combine the diversity seen within primate positional behavior, ecology, and morphology into a unified conceptual framework.

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