

Locomotor behavior in Ugandan monkeys

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Introduction

Studies of positional behavior have helped our understanding of postcranial adaptation in primates and this in turn has contributed to discussions concerning how and why particular directions in primate evolution occurred. At first, anatomists observed positional behavior, whether in captivity or in the wild, in order to describe what primates actually do. These observations led to simple categorization of primate species into, for example, brachiators or arboreal quadrupeds, as well as evolutionary scenarios reconstructing adaptive pathways in primate and human locomotor evolution (e.g. Keith, 1923; Clark, 1959; Napier and Walker, 1967). With the proliferation of field studies, many of the early categories proved less than useful and the association between particular anatomical features and specific behaviors came under closer scrutiny (e.g. Stern and Oxnard, 1973; Mittermeier and Fleagle, 1976; Morbeck *et al.*, 1979). These works, which used more sophisticated methods, specifically the quantification of primate positional behavior, helped to direct studies of positional behavior towards ecology as well as morphology. Despite these efforts made in the 1970s, surprisingly few species have been adequately sampled quantitatively in the wild, and, perhaps more importantly, very few studies have focused upon a particular research problem (for example, changes in body size and its effect on arboreal locomotion; Napier, 1967; Cartmill, 1974; Fleagle and Mittermeier, 1980; Fleagle, 1985; Jungers, 1985). Thus, how and why primates make the day-to-day choices they do, as well as why species are adapted to particular environments, are particularly central questions today, and few answers are to be found in the literature on positional behavior.

With this in mind, we began a field project in 1990 in Kibale Forest, Uganda, to examine positional behavior, body size, and habitat use in five

sympatric cercopithecoid monkey species (Gebo and Chapman, 1995a). We wanted first to identify the distinctive locomotor abilities of each species and second, to test relationships between positional behavior, body size, and habitat use. Fleagle and Mittermeier (1980) had noted several trends in South American monkey locomotion and we wondered whether African monkeys might conform to these same tendencies (e.g. smaller primates showing higher leaping frequencies and less use of the mid- and upper canopy). The five cercopithecoid species (*Cercopithecus ascanius*, *C. mitis*, *Lophocebus albigena*, *Colobus badius*, and *C. guereza*) are sympatric within the primary forest. Their sympatry and close taxonomic relationship minimize problems associated with comparing animals with very different anatomy, or living in different habitats. We also recorded locomotor behavior of one species, the red colobus monkey (*C. badius*), in a variety of ecological contexts, thus providing an overall assessment of its locomotor variation. We sampled behavior within the same season in different years, within different seasons of the same year, and within three different forest settings – primary, secondary, and pine forests (Gebo and Chapman, 1995b). We also sampled locomotor behavior of red colobus monkeys in crisis situations (i.e. when responding to predators) (Gebo *et al.*, 1994).

Methods

The Kibale Forest Reserve (560 km²) is situated in western Uganda, near the base of the Ruwenzori Mountains. It is a moist, evergreen forest with the canopy generally 25–30 m in height (Struhsaker, 1975; Kasenene, 1980; Skorupa, 1986, 1988; Kalina, 1988; Butynski, 1990). Parts of the reserve are comprised of swamp, grassland, plantations of pine, thicket, and colonizing forest (Butynski, 1990). The study site, Kanyawara, is situated at an elevation of 1500 m. Besides the species included in this study, the forest is inhabited by three strepsirrhine primates (*Galagoides demidovii*, *Galago inustus*, and *Perodicticus potto*), chimpanzees (*Pan troglodytes*) and three other cercopithecoid monkeys (*Cercopithecus aethiops*, *Cercopithecus lhoesti*, and *Papio hamadryas anubis*).

The positional behavior of the five species was observed in primary forest during the dry seasons (May–August) of 1990 and 1991. Additional observations on *Colobus badius* were made in secondary and pine forests, and during the wet season of 1990. All study populations were habituated to observers, although no animals could be approached closer than three meters. When approached, most individuals settled down to their normal regime after an initial moment of uncertainty. A focal animal technique of

Table 18.1. *Definitions of positional activities*

Locomotion

Quadrupedalism: all four limbs move in a regular pattern above a support or on the ground; includes walking, running, and galloping.

Leaping: the hindlimbs propel an animal across a gap. A leap 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.

Climbing: a movement up or down a vertical or steeply inclined support or through irregular and intertwined small supports; 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.

Other: includes, *quadrupedal suspensory movements*, in which the body is progressing below a support using three or four limbs; *bridging*, where spatial gaps are crossed by body stretching; *bimanualism*, in which the hands grasp a support and are used to pull the body up to a support from below (bimanual pull-up); *bipedalism*, in which only the hind feet are used to take a short walk; and *vertical bounding*, a succession of short jump-clings up a vertical support.

Postures

Sitting: animal supports weight on its haunches; feet may or may not be in contact with the support, above or below the body, legs splayed or close to midline.

Standing: animal stands on all four limbs.

Reclining: animal lies on its belly, side, or back.

Other: includes, *vertical clinging*: animal clings to a vertical support without sitting; *quadrupedal suspension*: animal hangs underneath a support by all four limbs; *bimanual suspension*: animal hangs from hands, usually with bent elbows; *hindlimb suspension*: animal hangs from feet; *bipedal stand*: animal stands on hindfeet, usually with the heel elevated above the support.

continuous sampling (Altmann, 1974) was used, and more than 20 adult individuals of each species were sampled. Positional behaviors were defined as shown in Table 18.1, and were recorded as a series of bouts. Each bout included a single behavior, bounded by a different posture or movement (see Fleagle, 1976; Fleagle and Mittermeier, 1980; Susman, 1984; Gebo, 1992). Animals were observed continuously from first contact until approximately 500 positional bouts were recorded for the day (between 7 and 9 hours of observation). Most types of locomotion and postures used by cercopithecoid monkeys are described and illustrated in Ripley (1967), Morbeck (1975), Mittermeier and Fleagle (1976), Fleagle (1978, 1980), and Rose (1979).

The behavioral context of each observation was recorded as *travel* (long distance movements between trees, usually between a series of trees, from or to feeding or resting sites), *feeding* (movements within a single tree), or *resting* (periods of inactivity). The circumference of the support used was recorded as *large* (>25 cm), *medium* (6–25 cm), or *small* (<5 cm); its location within the canopy as within the *upper* (>16 m above ground level), *middle* (5–15 m) or *lower* (<5 m) zone, and its orientation as *horizontal* (0–15° from horizontal), *oblique* (15–75°) or *vertical* (75–90°).

Results

Positional behavior (Fig. 18.1)

Cercopithecus ascanius preferred to move by climbing and quadrupedalism, while *C. mitis* was predominately quadrupedal. Neither of the guenons frequently used quadrupedal suspensory movements, bridging, bimanualism, bipedalism, or vertical bounding ("Other" in Fig. 18.1). Their frequencies of sitting and standing were similar. *Lophocebus albigena* had a locomotor and postural profile similar to that of blue monkeys, but leapt more frequently. Both *Colobus* species leapt more often than any of the cercopithecines. *Colobus guereza* was the most frequent leaper and the least frequent climber. Bounding and galloping along horizontal, usually large diameter supports was observed more often in the guereza than in the red colobus (see also Morbeck, 1975, 1976, 1977, 1979; Mittermeier and Fleagle, 1976; Rose, 1978, 1979). When stationary, *C. badius* preferred to sit or stand, while *C. guereza* preferred sitting and reclining postures.

The smallest species, *Cercopithecus ascanius*, climbed most frequently and leapt rather infrequently compared to the other four species, while *Colobus guereza*, the largest species, leapt the most and climbed least often. *Cercopithecus mitis* climbed at approximately the same frequency as the larger *L. albigena*. Both colobines leapt more frequently than the similarly sized mangabey, which leapt as much as the smaller *C. ascanius*. It is evident that differences in body size among these species do not correspond closely to differences in locomotor frequency, although there is a tendency for size to correlate negatively with frequency of climbing, and positively with that of leaping.

Figure 18.2 compares male and female locomotor frequencies. Quadrupedalism differs between the sexes by no more than four percentage points in all five species. The frequency of climbing typically shows a difference of less than two percentage points, while leaping varies by four

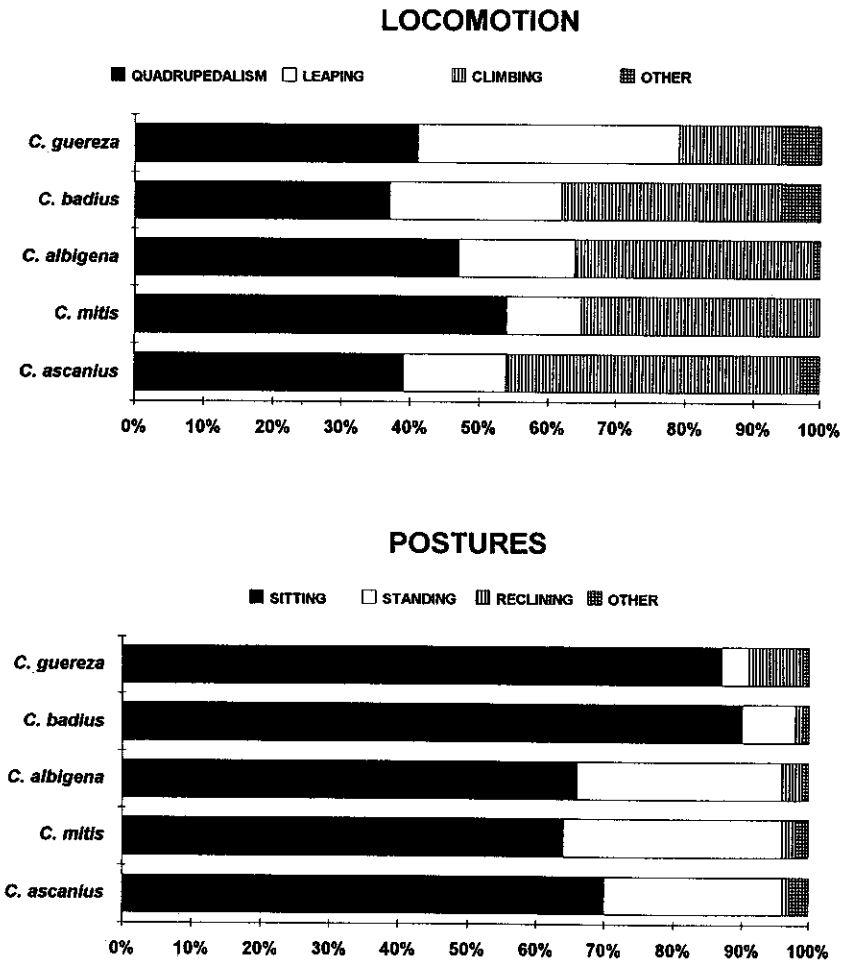


Fig. 18.1. Locomotor and postural frequencies.

percentage points or less. Thus, no appreciable locomotor differences associated with sex can be documented in these sexually dimorphic species.

Habitat and support use

All five species were observed in each of the three height zones (Fig. 18.3). With the exception of *Colobus guereza*, which used the upper zone most often, all species preferred the middle zone. *Colobus badius*, and to a lesser extent *L. albigena*, was observed in the middle and upper zones about equally often. Guenons clearly preferred the middle zone over the upper,

LOCOMOTION BY SEX

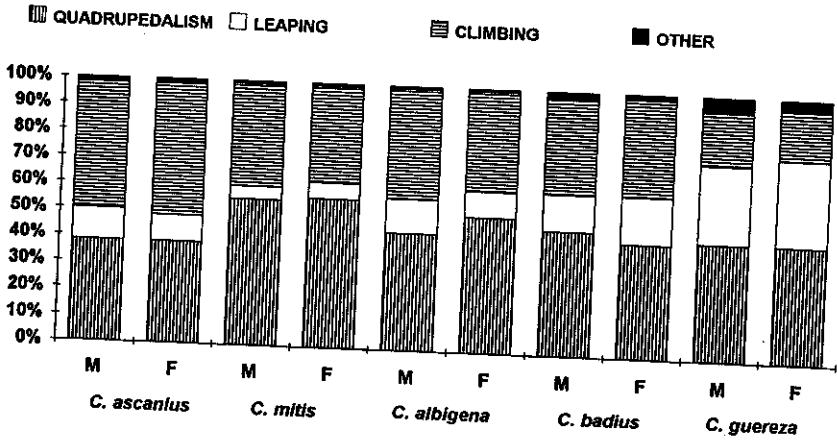


Fig. 18.2 Locomotion by sex and species (M: males; F: females).

CANOPY HEIGHT

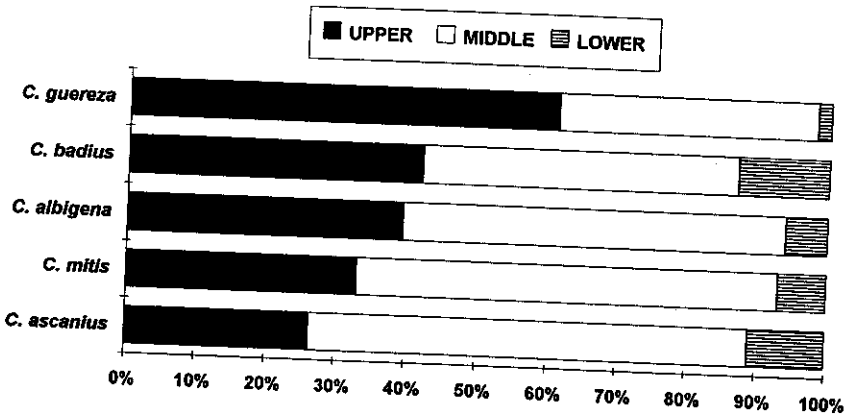


Fig. 18.3. Canopy use.

while *Cercopithecus ascanius* and *Colobus badius* were observed in the lower zone more frequently than the other species. All five species were observed to come to the ground occasionally.

All five species used medium sized supports approximately half to two-thirds of the time. *Cercopithecus ascanius*, the lightest species, used the smallest supports most often, while *Colobus guereza*, the heaviest, used the largest supports most frequently. Beyond this simple correspondence, associations with body weight are less clear. *Lophocebus albigena*, for example,

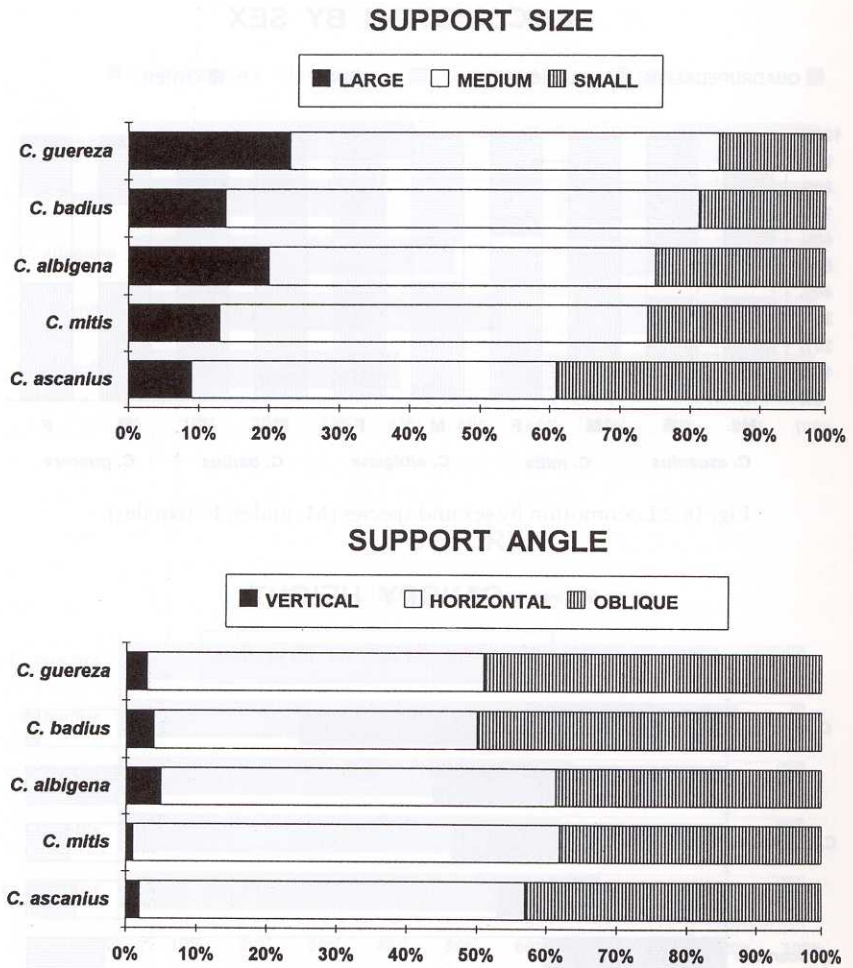
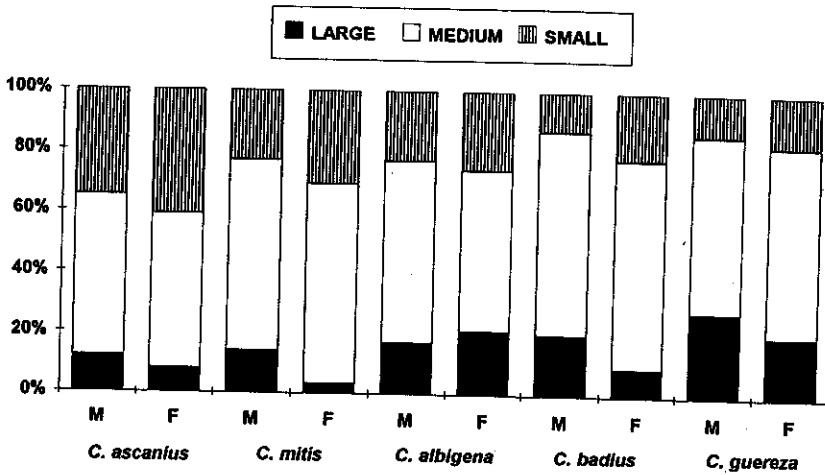


Fig. 18.4. Support use by size and orientation.

used the largest supports more often than the heavier *C. badius*, and all five species preferred medium sized supports.

All five species were observed on all three types of supports (horizontal, oblique, and vertical), and all used vertical supports least often (Fig. 18.4). The three largest species, *L. albigena*, *C. badius*, and *C. guereza*, used vertical supports more often than did the smaller guenons. The cercopithecines preferred horizontal supports while the colobines used horizontal and oblique supports about equally often. Separating movements from postures showed little variation in support use across species.

SUPPORT SIZE BY SEX



SUPPORT ANGLE BY SEX

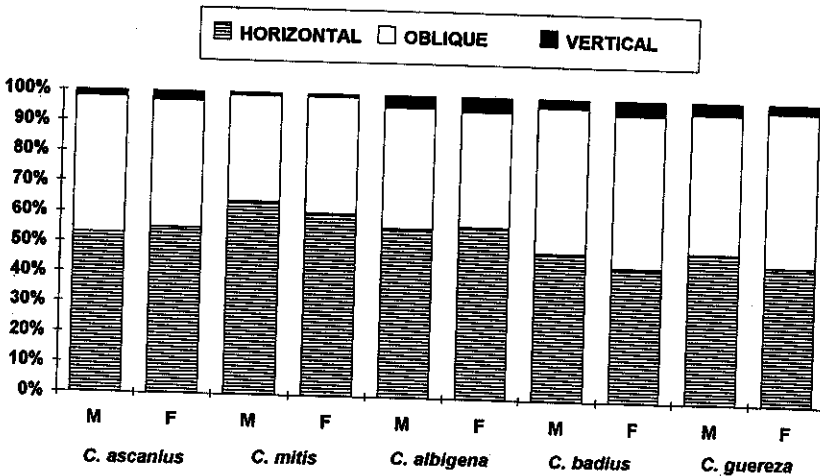


Fig. 18.5. Use of different support sizes and orientations by sex and species.

As shown in Figure 18.5, there is little or no evidence of intraspecific variation in support use associated with sex in these species, and the slight differences that are seen are not associated with the species' degree of sexual dimorphism in body size. The smaller-sized females do use large supports slightly less often and small supports slightly more often than do males of

the same species (but see *L. albigena*, Fig. 18.5). Sex differences are most marked in *C. badius*, the least dimorphic species in terms of its body size (Table 18.2), but in no species are the sex differences very dramatic. The use of supports of different orientation likewise shows little association with sex within species. The biggest difference is observed in *C. guereza* where females use oblique supports more frequently than do males.

From data derived by scanning of the spatial position of individuals at 10-minute intervals (Gebo and Chapman, 1995a), it is evident that the crown of the tree was used more often than the major branches or the trunk, with two exceptions. *Lophocebus albigena* utilized the crown only slightly more frequently than the major branches, while *C. guereza*, on the other hand, showed a decided preference for major branches.

Habitat and seasonal effects on positional behavior of red colobus monkeys

We compared the positional behavior of *C. badius* during the dry season in primary and secondary forest. Secondary forest is distinguished from primary forest in being less continuous. Large open stretches between trees are common. During travel, quadrupedalism was more frequently observed in secondary forest than in primary forest. During feeding, quadrupedalism was also more often observed in secondary forest, as is the case for leaping, while climbing decreases dramatically within secondary forest (Fig. 18.6). We also observed *C. badius* in a mature pine plantation, a very different type of forest. Here, trees were spaced very close together and small branches tended to break when red colobus monkeys walk out away from the trunk. Locomotor frequencies during travel differed by no more than five percentage points between pine and secondary forests. In feeding, quadrupedalism and leaping were more frequent in the pine forest, while climbing decreased substantially. Overall, red colobus monkeys utilized quadrupedalism, leaping, and climbing more equally in the pine plantation than in primary and secondary forests. Quadrupedalism is used most extensively in secondary forests. The largest observed differences in locomotor frequencies among the different forests occurred during feeding (Fig. 18.6).

We also compared positional behavior of red colobus monkeys in primary forest during the dry and wet seasons of 1990. The data show a five and six percentage point difference in frequencies of quadrupedalism and leaping during travel (Fig. 18.6). Locomotion associated with feeding, however, shows a twenty-one percentage point decrease in quadrupedalism in the wet season, and a compensatory increase of nine and eight percentage points for leaping and climbing, respectively. Clearly, seasonal effects

Table 18.2. Body weights (kg) and number of bouts observed for each species

	<i>Cercopithecus ascanius</i>	<i>Cercopithecus mitis</i>	<i>Lophocebus albigena</i>	<i>Colobus badius</i>	<i>Colobus guereza</i>
Male body weight	4.2	6.0	9.0	8.3	10.1
Female body weight	3.0	3.5	6.4	8.2	8.0
Male:female weight ratio	1.4	1.7	1.4	1.0	1.3
Mean female and male	3.6	4.8	8.0	8.25	9.1
Total bouts	6,450	6,444	6,165	7,515	6,452

Source: Body weights from Waser (1987) and Fleagle (1988).

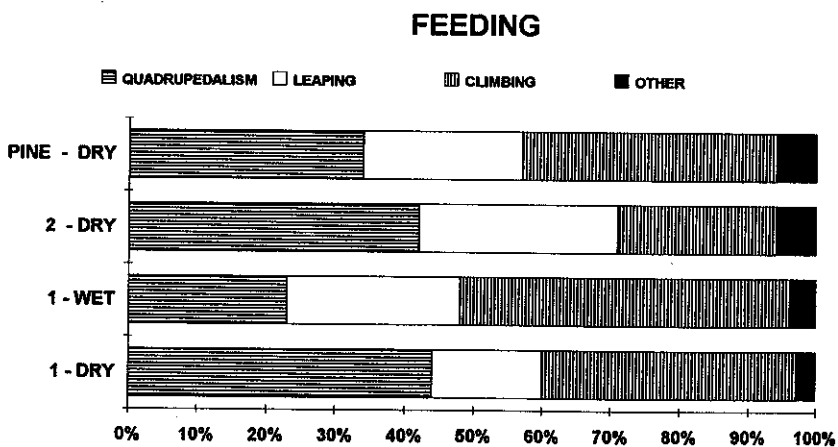
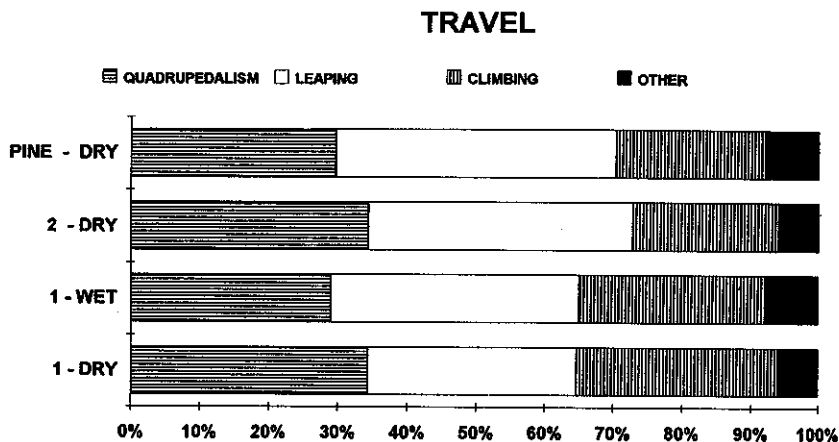


Fig. 18.6. Use of forest types (primary, 1; secondary, 2; and pine) for travel and feeding by red colobus monkeys, in wet and dry seasons.

on locomotor behavior are greater than the effects of forest type, and are especially marked during feeding.

The effects of predation threat upon locomotion in red colobus monkeys

Two approaches were utilized to study the effects of the apparent presence of a predator upon locomotor frequencies. We simulated the approach of a potential terrestrial predator by moving towards unhabituated groups of

PREDATOR RESPONSE

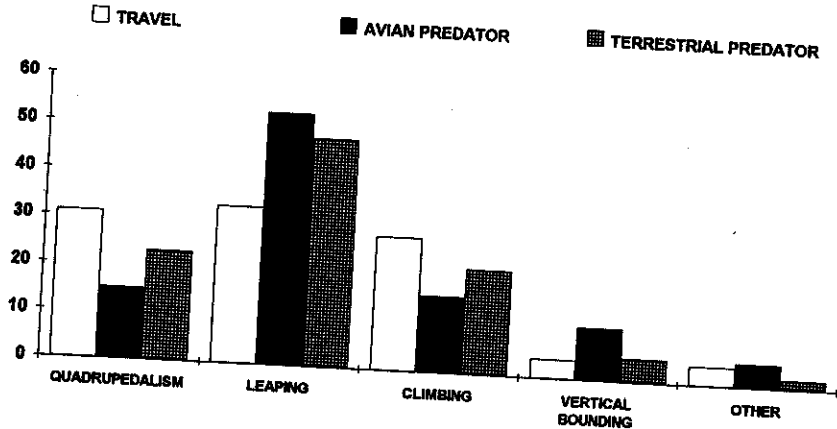


Fig. 18.7. Locomotor responses of red colobus to different predator situations, compared to normal locomotion during travel.

red colobus monkeys and scored their fleeing responses. Second, we played calls of the crowned hawk eagle (*Stephanoaetus coronatus*) to red colobus groups and again scored their fleeing movements (see Gebo *et al.*, 1994, for details). Comparing the escape movements in the two situations (terrestrial and avian “predator”) to “normal” travel movements shows that quadrupedalism and climbing decreased, while leaping increased dramatically (Fig. 18.7). Of the rarer locomotor behaviors, only vertical bounding increased substantially, during playback of the crowned hawk-eagle call (Fig. 18.7).

The linear distance moved during a bout was also affected by the fleeing responses provoked by the crowned hawk-eagle call. Longer mean distances, higher maximum distances, and more frequent use of long distance movements occurred (Gebo *et al.*, 1994). In contrast, responses to the “terrestrial predator” showed distance measures similar to those observed during “normal” travel.

In summary, leaping increased in frequency in times of crisis, and obviously represents a strategy for rapidly crossing large distances. Of the two simulated predators, the hawk-eagle provoked more substantial changes in locomotor behavior, perhaps indicating that these predators pose a greater threat (see Leland and Struhsaker, 1993).

Discussion and conclusion

The results of the Kibale Forest project show that all five species commonly utilize five varieties of positional behavior (quadrupedalism, climbing, leaping, sitting, standing), and that each species displays a distinctive pattern of use for these five behaviors. Canopy, crown, and support use are fairly similar across the five species. Positional behavior shows much greater interspecific difference during feeding than during travel. The smaller species tend to climb more and leap less often than the larger species – the exact reverse of the trend documented for sympatric platyrrhines (Fleagle and Mittermeier, 1980). On the other hand, intraspecific body size differences due to sexual dimorphism are not manifested in obvious differences in the frequencies of positional behavior, or in the use of supports of different size and orientation.

The study of red colobus monkeys in different forests, in different seasons, and in the predator experiments shows that substantial changes in locomotor frequencies can occur, especially during feeding or times of crisis. This series of observations demonstrates that this primate species, and probably primates in general, are ecologically flexible in their use of positional behavior (see also Crompton, 1984; Boinski, 1989; Doran and Hunt, 1994; Dagosto, 1995; Doran, 1996; Dagosto and Yamashita, 1998) and that intraspecific variation is an important consideration when attempting to sort out interspecific comparisons (in contrast to Garber and Preutz, 1995; McGraw, 1996). We believe that individual primates are making movement choices according to a number of current and past factors. Anatomical design and body size affect movement possibilities while food and predators change seasonally throughout the life of a primate. Thus to truly understand primate positional behavior, we need to quantify intraspecific variation. This means better sampling over longer time periods, in different seasons, and if possible, in different habitats. Increased sampling will help to ensure that the "movement sample" adequately addresses the particular problem at hand. What are the major problems? First, positional studies need to determine how movements and arboreal pathways are linked and why. Second, how do primate activities (e.g. feeding behavior) affect locomotor abilities? Third, how does size affect positional behavior? In the end, we need to understand cause and effect.

Traditionally, positional studies have played a central role in determining locomotor adaptation among fossil primates. Given the number of fossil discoveries over the past decade, positional studies will continue to play an

important role in these evolutionary debates. If we truly want to understand how and why living and extinct primates move, we believe that we need to renew our emphasis on field work to help alleviate the many behavioral, ecological, and anatomical concerns that exist in the field today.

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