

Habitat, Annual, and Seasonal Effects on Positional Behavior in Red Colobus Monkeys

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ABSTRACT Positional behavior in adult red colobus monkeys (*Colobus badius*) was examined in a variety of ecological contexts. Using a focal-animal methodology, we assessed how data collected by different observers, in different years, in different seasons, and in different forests affected estimates of positional behavior. In all, 23,000 bouts were recorded. Variation in frequency is greatest in the common behaviors, especially arboreal quadrupedalism. Significant behavioral differences occur more often in the context of different forests than in annual or seasonal comparisons. The activity of feeding exhibits the largest frequency changes across positional behavior and ecological context. In all, red colobus monkeys exhibit substantial amounts of flexibility in positional behavior across different ecological contexts.

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One of the major problems in evaluating data on primate positional behavior has been the lack of assessment of variation in different ecological contexts. The study of this variation is, however, vital, because it provides a yardstick to evaluate the biological significance of interspecific variation. If the variation exhibited by a single species in different contexts is large, then caution must be used in interpreting interspecific differences which are based on studies restricted to a single context. This is a largely unexplored aspect of primate positional behavior (but see Crompton, 1984; Dagosto, 1992; Garber and Pruetz, 1993; Dagosto and Yamashita, unpublished manuscript). This issue is part of a suite of methodological concerns that need to be addressed in future research in primate positional behavior. Other issues such as the diverse definitions for locomotor and postural behaviors (e.g., contrast Fleagle, 1976; Cant, 1986, 1988; Fontaine, 1990; Hunt, 1992) and the variety of different techniques used in the field to quantify positional behavior (e.g., Boinski, 1989) all need to be more fully evaluated (see Doran, 1992).

This study provides quantitative data on locomotor and postural variation and assesses how a single primate species (*Colobus badius*) utilizes its repertoire of positional behavior in different ecological contexts within Kibale Forest, Uganda. We sampled positional behavior in the same season but in different years, in different seasons of the same year, and in three different forests—primary, secondary, and pine. We also examined the problem of interobserver sampling error. In all of these diverse settings, over 23,000 bouts of positional behavior were collected on red colobus monkeys.

We expected to find small differences (<5%) in frequencies of positional behavior between groups due to habitat or seasonal changes. We further expected that seasonal differences in resources would result in small changes in positional frequencies during feeding. In contrast, we expected frequencies during travel to be more conserva-

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tive since primates move through the same canopy in all seasons.

Assumptions about the conservative nature of primate positional behavior are implicit in the realm of comparative morphology. Differences in anatomical features are often associated with differences in locomotor behavior between species (e.g., Fleagle, 1977; Fleagle and Meldrum, 1988). Some of these studies are based on a single positional study in a single season and habitat. Do such studies provide us with a reliable sample on which to base form-function complexes? This paper attempts to quantify positional behavior in different ecological contexts for a single species to determine the amount of variation we should expect to see in different ecological settings.

METHODS

Environment

The Kibale Forest Reserve (560 km²), located in western Uganda, is a moist evergreen forest with a canopy generally 25–30 m high, although some trees may exceed 55 m (Wing and Buss, 1970; Struhsaker, 1975; Butynski, 1990). The remainder of the reserve is composed 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 1,500 m.

The positional behavior of the red colobus monkey was studied in three areas of the reserve which are characterized by different histories of logging. The K30 forestry compartment is a relatively undisturbed and mature forest (Skorupa, 1988). The K14 compartment had approximately 5.1 stems/ha of 23 species removed between May and December 1969, however our observations were conducted in a relatively undisturbed section of this compartment, thus the groups that used the K30/K14 areas are considered to use “pristine” forest. The K15 compartment was logged between September 1968 and April 1969, and a total of 7.4 stems/ha from 18 species were extracted (Skorupa, 1988). We observed groups using a heavily disturbed section of this compartment and these groups are con-

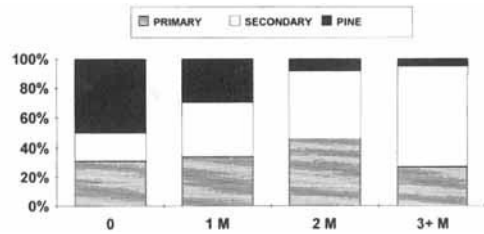


Fig. 1. Distances between branches of adjacent trees (gap distances). Two 600-m transects through each of the three types of forests were used to measure the distances between branches of adjacent trees and thus document the linear length in meters and frequency of gaps between trees. Saplings were excluded. Note that the pine plantation and primary forest exhibit fewer gaps (more continuous forest) than is the case for secondary forest.

sidered to be using “secondary” forest. Within K14/K30, *Diospyros abyssinica* (12%), *Markhamia platycalyx* (12%), *Celtis durandii* (11%), *Uvariopsis congensis* (10%), and *Bosqueia phoberus* (9%) make up the most common trees. In the K15 forestry compartment, trees such as *Diospyros abyssinica* (17.5%), *Markhamia platycalyx* (12.7%), *Celtis durandii* (9.7%), and *Funtumia latifolia* (8.7%) are common. The third habitat that was sampled was a pine plantation, planted with a number of different pine species in the 1960s.

In each forest type, 600-m transects were sampled to determine the number and length of spatial gaps between adjacent trees (Fig. 1). Along the primary forest transects, the average distance between the branches of adjacent trees is 1.2 m, and 42% of the primary forest is continuous. Seventy-four percent of the primary forest possesses gaps of 1 m or less, while gaps of 2 m or less represent 90% of the spatial distances between trees. Large gaps in excess of 5 m occur in only 2% of primary forest.

In secondary forest, the average distance between trees is 2.1 m, and only 25% of the secondary forest is continuous. Fifty-nine percent of adjacent trees had gaps of 1 m or less. Two-meter gaps (Fig. 1) as well as 10- to 20-m open stretches are more commonly observed in secondary forest. Large gaps in excess of 5 m occur in 12% of our sample of secondary forest.

TABLE 1. Annual and ecological comparisons of locomotor behavior in the red colobus monkey (*Colobus badius*) during the activities of travel and feeding (Kibale Forest, Uganda)

| | 1° Forest Dry season | | Wet season 1990 | 2° Forest Dry season 1991 | Pine forest Dry season 1990 |
|--------------------------|-------------------------|-------|--------------------|---------------------------------|-----------------------------------|
| | 1990 | 1991 | | | |
| Travel | | | | | |
| Quadrupedalism | 34% | 26% | 29% | 34% | 30% |
| Leaping | 30 | 39 | 36 | 38 | 41 |
| Climbing | 29 | 26 | 27 | 21 | 22 |
| Other | 6 | 9 | 8 | 6 | 8 |
| Bouts | 3,204 | 1,470 | 1,064 | 1,515 | 1,515 |
| Feeding | | | | | |
| Quadrupedalism | 44% | 28% | 23% | 42% | 34% |
| Leaping | 16 | 20 | 25 | 29 | 23 |
| Climbing | 37 | 45 | 48 | 23 | 37 |
| Other | 3 | 7 | 4 | 6 | 6 |
| Bouts | 1,745 | 1,707 | 857 | 1,282 | 782 |
| Total locomotor behavior | | | | | |
| Quadrupedalism | 25% | 18% | 17% | 26% | 20% |
| Leaping | 17 | 19 | 20 | 23 | 22 |
| Climbing | 21 | 24 | 23 | 15 | 17 |
| Other | 3 | 5 | 4 | 4 | 5 |
| Total bouts | 7,515 | 4,863 | 3,007 | 4,143 | 3,563 |
| Locomotor/total bouts | 66% | 66% | 64% | 68% | 64% |
| Observation hours | 97 | 80 | 48 | 63 | 55 |

In the pine plantation, trees are very close together with an average gap distance of 0.5 m. Sixty-eight percent of this pine plantation is continuous with 94% of the trees being within 1 m from each other. Spatial gaps of over 5 m occur in only 2% of the distance between adjacent trees.

Sampling behavior

To make reasonable assessments of positional behavior, we believed that a minimum of 3,000 positional bouts would be needed for each ecological context. We arrived at 3,000 bouts from our positional study on five Kibale Forest monkeys which showed that frequency changes are greatly reduced after 3,000 positional bouts are recorded (see Fig. 1 in Gebo and Chapman, 1994). A bout is defined as a change in positional behavior (Fleagle, 1976; Fleagle and Mittermeier, 1980; Susman, 1984; Gebo and Chapman, 1994). In this study, the number of bouts per context ranges from 3,007 to over 7,000 bouts (Table 1). Locomotor to postural bouts run about 2 to 1; thus 3,000 positional bouts represent about 2,000 locomotor bouts. This study represents over 300 hours of actual observation time (Table 1).

All of the positional behaviors (e.g., arboreal quadrupedalism, climbing, leaping, sit-

ting, and standing) are described in detail in Gebo and Chapman (1994) and these five behaviors represent the most common positional behaviors for *Colobus badius*. Walking and running are lumped together under the category of quadrupedalism while clambering and vertical climbing are lumped under climbing. "Other" in Table 1 consists of rare or infrequent movements like bipedalism, vertical bounding, bimanualism, and quadrupedal suspensory movements. Each positional behavior was recorded in the context of one of two activities (travel—movements between trees; and feeding—movements within a single tree), as well as with respect to the physical structure (size and orientation), and the location of the support (height in canopy; Table 2).

A focal-animal technique of continuous sampling was used throughout the study on adult animals (Altmann, 1974). Adult animals were observed continuously from first contact until approximately 500 positional bouts were recorded for that day. When a focal animal was lost from view, we switched to another adult animal.

To evaluate interobserver reliability, four trained observers followed the same adult animal and recorded positional behavior over the same length of time, approximately

TABLE 2. Use of supports (angle, size, and height in the canopy) by forests and seasons for red colobus monkeys of Kibale Forest, Uganda¹

| Primary forest—dry season 1990 | | | | | | | | | | | |
|----------------------------------|-----|-----|----|-------|-----|-----|-----|-------|-----|-----|-----|
| N | H | O | V | N | UC | MC | LC | N | L | M | S |
| 7,468 | 46% | 50% | 4% | 7,483 | 42% | 45% | 13% | 5,969 | 14% | 68% | 19% |
| Primary forest—dry season 1991 | | | | | | | | | | | |
| N | H | O | V | N | UC | MC | LC | N | L | M | S |
| 4,861 | 35% | 63% | 2% | 4,862 | 42% | 55% | 3% | 4,862 | 8% | 52% | 41% |
| Primary forest—wet season 1990 | | | | | | | | | | | |
| N | H | O | V | N | UC | MC | LC | N | L | M | S |
| 3,002 | 34% | 63% | 3% | 3,002 | 15% | 84% | 1% | 3,002 | 9% | 73% | 18% |
| Secondary forest—dry season 1991 | | | | | | | | | | | |
| N | H | O | V | N | UC | MC | LC | N | L | M | S |
| 3,696 | 47% | 50% | 4% | 3,827 | 37% | 60% | 2% | 3,722 | 8% | 65% | 26% |
| Pine forest—dry season 1991 | | | | | | | | | | | |
| N | H | O | V | N | UC | MC | LC | N | L | M | S |
| 3,562 | 40% | 51% | 9% | 3,562 | 24% | 73% | 2% | 3,554 | 6% | 91% | 3% |

¹N = sample size; H = horizontal support ($\pm 15^\circ$ to the horizontal); O = oblique support (between 15 and 75° to the horizontal); V = vertical support ($\pm 15^\circ$ to the vertical); UC = upper canopy (16–25+ m); MC = middle canopy (6–15 m); LC = lower canopy (0–5 m); L = large-sized support (>25 cm in circumference); M = medium-sized support (between 6–25 cm in circumference); S = small-sized support (<5 cm in circumference).

TABLE 3. Interobserver observations (%) on positional behavior for a single adult red colobus monkey (3 hours)¹

| | Observer | | | | Range |
|-------------------|----------|------|------|------|-------|
| | 1 | 2 | 3 | 4 | |
| Quadrupedalism | 15.4 | 14.9 | 15.7 | 18.6 | 3.7 |
| Leaping | 19.9 | 17.0 | 19.3 | 17.3 | 2.9 |
| Climbing | 19.9 | 17.7 | 16.4 | 15.9 | 4.0 |
| Bimanualism | 3.2 | 4.3 | 5.0 | 3.8 | 1.8 |
| Bridging | 1.4 | 1.4 | 1.4 | 1.4 | 0.0 |
| Vertical bounding | 4.5 | 5.7 | 5.0 | 5.0 | 1.2 |
| Sitting | 35.3 | 38.3 | 36.4 | 37.8 | 3.0 |
| Vertical clinging | 0.7 | 0.7 | 0.7 | 0.7 | 0.0 |
| Bouts | 156 | 141 | 140 | 156 | 16.0 |

¹Average absolute difference using observer 1 as the standard = 1.3%; average difference (with \pm sign) = 0.05%.

3 hours. When our focal animal was lost, all observers switched to another adult animal and continued the process of data collection. Table 3 presents the results of this test.

Statistics

The problem of independence for this type of data collection is profound since one behavior performed at a single instance in time is dependent on the behavior just performed. Thus, for statistical comparisons, we divided the entire data set into 100-bout segments, and for each segment, we determined a positional behavior profile and used these profiles as an independent data point in an analysis of variance (ANOVAs). Subsequently to insure independence, we systematically removed every second segment and used each second unit in statistical comparisons between positional behavior and ecological contexts. By reporting tests both with and without removing every second

segment, 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 ANOVA and examined individual pairwise differences using a Scheffé Test. The Scheffé Test allows us to contrast all possible pairs of group means from our ANOVA by making post hoc comparisons. 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 statistical significance, differences have to be rather substantial (Table 4).

RESULTS

Interobserver reliability

The common positional behaviors can differ in frequency by as much as 3 or 4% between observers, while the rarer behaviors differ by only 1 or 2% (Table 3). Estimates of

TABLE 4. Statistical comparisons of *Colobus badius* positional behavior profiles, recorded in different habitats, seasons, or years (ANOVA—Scheffé Test)¹

| | | | | | |
|---------------------------------------|----------|----------|----------|----------|---|
| Quadrupedalism | 1 | 2 | 3 | 4 | 5 |
| 1. Primary forest, dry season, 1990 | | | | | |
| 2. Primary forest, dry season, 1991 | * | | | | |
| 3. Primary forest, wet season, 1990 | <u>*</u> | | | | |
| 4. Secondary forest, dry season, 1991 | * | | | | |
| 5. Pine forest, dry season, 1990 | | <u>*</u> | <u>*</u> | * | |
| Leaping | 1 | 2 | 3 | 4 | 5 |
| 1. Primary forest, dry season, 1990 | | | | | |
| 2. Primary forest, dry season, 1991 | | | | | |
| 3. Primary forest, wet season, 1990 | | | | | |
| 4. Secondary forest, dry season, 1991 | | | | | |
| 5. Pine forest, dry season, 1990 | <u>*</u> | | | | |
| Climbing | 1 | 2 | 3 | 4 | 5 |
| 1. Primary forest, dry season, 1990 | | | | | |
| 2. Primary forest, dry season, 1991 | | | | | |
| 3. Primary forest, wet season, 1990 | | | | | |
| 4. Secondary forest, dry season, 1991 | | <u>*</u> | * | | |
| 5. Pine forest, dry season, 1990 | <u>*</u> | <u>*</u> | <u>*</u> | | |
| Bimanualism | 1 | 2 | 3 | 4 | 5 |
| 1. Primary forest, dry season, 1990 | | | | | |
| 2. Primary forest, dry season, 1991 | | | | | |
| 3. Primary forest, wet season, 1990 | | | | | |
| 4. Secondary forest, dry season, 1991 | <u>*</u> | <u>*</u> | * | | |
| 5. Pine forest, dry season, 1990 | | | | <u>*</u> | |
| Vertical bounding—no significance | | | | | |
| Sitting | 1 | 2 | 3 | 4 | 5 |
| 1. Primary forest, dry season, 1990 | | | | | |
| 2. Primary forest, dry season, 1991 | | | | | |
| 3. Primary forest, wet season, 1990 | | | | | |
| 4. Secondary forest, dry season, 1991 | | | | | |
| 5. Pine forest, dry season, 1990 | * | * | * | | |
| Vertical Clinging | 1 | 2 | 3 | 4 | 5 |
| 1. Primary forest, dry season, 1990 | | | | | |
| 2. Primary forest, dry season, 1991 | | | | | |
| 3. Primary forest, wet season, 1990 | | | | | |
| 4. Secondary forest, dry season, 1991 | <u>*</u> | <u>*</u> | * | | |
| 5. Pine forest, dry season, 1990 | | | | * | |
| Standing—no significance | | | | | |
| Bipedal standing—no significance | | | | | |
| Recline | 1 | 2 | 3 | 4 | 5 |
| 1. Primary forest, dry season, 1990 | | | | | |
| 2. Primary forest, dry season, 1991 | | | | | |
| 3. Primary forest, wet season, 1990 | | | | | |
| 4. Secondary forest, dry season, 1991 | | | | | |
| 5. Pine forest, dry season, 1990 | | | <u>*</u> | | |

¹Asterisks represent statistically significant differences (0.05 level) between pairwise comparisons for all 100 bout intervals. Underlined asterisks represent statistical significance for every other 100 bout interval.

climbing and quadrupedalism varied the most, about 4%, with differences in sitting and leaping being 3%. The average absolute difference between observers was 1.3%. The overall difference in the number of bouts recorded by the different observers was about 10%. Thus, although some observers clearly miss behaviors relative to others, the overall effectiveness is fairly high and locomotor profiles are similar across observers.

Annual effects

In the dry seasons of 1990 and 1991 (primary forest), the frequencies for quadrupede-

alism (34% and 26%) and for leaping (30% and 39%) during travel differed by 8% and 9%, respectively (Table 1). During the activity of feeding, quadrupedalism differed by 16% from one year to the next while climbing differed by 8% (Table 1). Considering all activities, quadrupedalism again differed the most from one year to the next (a statistically significant difference, Table 4). Thus, of the three major types of movement utilized by *Colobus badius*, quadrupedalism is the most affected in an annual comparison, although large frequency differences are also evident for climbing and leaping (Fig. 2).

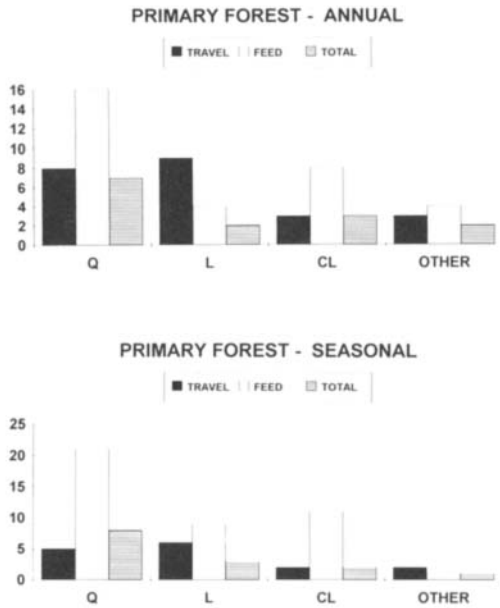


Fig. 2. Range of variation (percent differences) for quadrupedalism (Q), leaping (L), climbing (CL), and other within mature primary forest by year and season.

Seasonal effects

Comparing the dry and wet seasons of 1990 (primary forest) shows a 5% and 6% difference in locomotor frequencies for quadrupedalism and leaping during travel, respectively, a slightly smaller effect than in the annual comparison (Table 1; Fig. 2). During feeding, a 21% decrease in quadrupedalism is noted to occur in the wet season, as are increases of 9% and 8% for leaping and climbing, respectively. Positional behavior during all activities shows smaller increases in leaping and climbing frequencies in the wet season, with the biggest difference observed for quadrupedalism. Only the seasonal differences for quadrupedalism reach statistical significance (Table 4).

In contrast, locomotor frequencies in the primary forest for the dry seasons of 1991 and the wet season of 1990 show a similar pattern. Most differences are within 3% of each other with the largest differences (5%) being observed for quadrupedalism and leaping during feeding (Table 1).

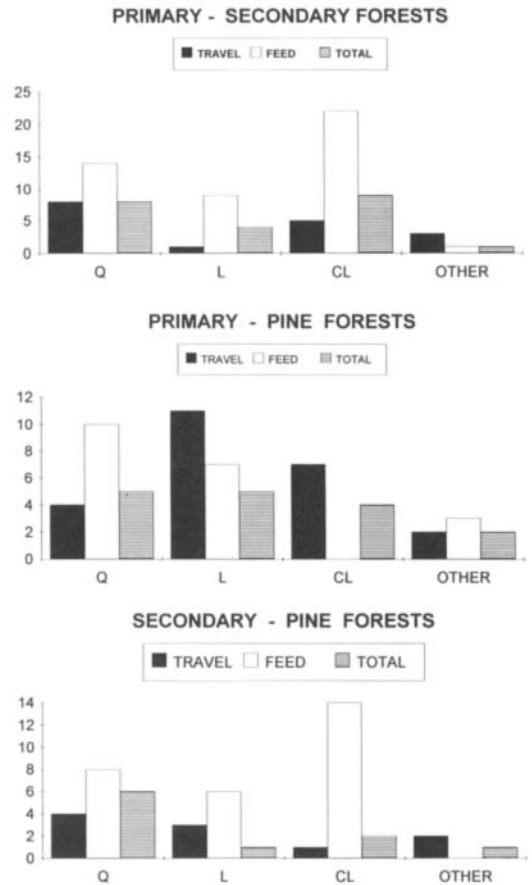


Fig. 3. Range of variation (percent differences) for quadrupedalism (Q), leaping (L), climbing (CL), and other by forest types (primary vs. secondary; primary vs. pine; and secondary vs. pine).

Forest types

Comparing locomotor behavior recorded in the 1991 dry seasons from primary, secondary, and pine forests shows a variety of differences (Table 1; Fig. 3). In comparing primary and secondary forest use, we found that quadrupedalism during travel is more frequently observed in secondary forest (+8%) than in primary forest, while leaping is less frequent (-5%). During feeding, quadrupedalism is more often observed in secondary forest (+14%), as is leaping (+9%), while climbing decreases dramatically (-22%). Combining travel and feeding shows quadrupedalism to increase in frequency, while climbing decreases, for red colobus monkeys in secondary forest (Table 1).

Second, within the pine plantation, no locomotor differences greater than 5% are observed during travel between pine and secondary forest use. For feeding, quadrupedalism (+8%) and leaping (+6%) increase, while climbing decreases substantially (-14%). Overall, red colobus monkeys within the pine plantation utilize quadrupedalism, leaping, and climbing more equally compared to the other two forest types (Table 1). Quadrupedalism is used more extensively in secondary forest. Again, behaviors exhibited during feeding show the largest frequency differences between forest types (Fig. 3).

Quadrupedalism within the pine plantation differs significantly from quadrupedalism in the primary and secondary forests (Table 4). Leaping also differs significantly between pine and primary forest (1990 dry season) use. In the pine forest, leaping during travel is especially high in frequency, 41% (Table 1; Fig. 3). Climbing in secondary forest differs significantly from climbing in primary forest, regardless of the season (Table 4). The use of bimanualism in secondary forest is statistically different from its use in primary or pine forests. The frequency of sitting also differs significantly between the pine and primary forests, regardless of the season. Reclining differs only between its use in pine and primary forests (1990 wet season). Vertical clinging is rarely used in secondary forests and thus is significantly different from its use in primary and pine forests (Table 4).

Tree use

In the primary forest (dry seasons), red colobus prefers to use medium-sized and oblique supports in the middle canopy (Table 2). Smaller supports as well as horizontal supports are used next in frequency. The dry season of 1991 shows greater use of small supports relative to the other ecological contexts (Table 2). Large or vertical supports as well as the lower canopy heights are rarely used in the dry seasons. The most frequent use of lower canopy heights is in the dry season of 1990 (13%, Table 2).

In the wet season (primary forest), there is a strong preference for medium-sized and oblique supports located especially in the

middle canopy (84%, Table 2). Comparing the wet and dry seasons of 1990 shows that oblique supports and the middle canopy are utilized more frequently in the wet season, while large-sized supports are used more often in the dry season (Table 2).

In secondary forest, horizontal and oblique supports are used about equally. This is also the case for the dry-season (1990) primary-forest data (Table 2). Medium-sized supports are preferred, but small supports are also often used. Use of supports by orientation is virtually identical in secondary and primary forests (dry season 1990). Use of the secondary forest canopy and support sizes are also similar to those for primary forest dry-season use.

In the pine forest, medium-sized supports as well as oblique supports located in the middle canopy are used most frequently. Medium-sized supports achieve their highest frequency of use within the pine plantation (91%, Table 2). The low frequency of use for small supports within pine trees is probably due to the fact that pine branches break more often than branches in other types of trees. When red colobus monkeys walk out and away from the trunk, pine branches tend to bend downward and break at the base. Thus, red colobus monkeys fall or scramble about more often in pine trees, and this may contribute to the more frequent use of bimanualism in the pine plantation. Use of vertical supports is also at its highest frequency in the pine plantation (9%, Table 2).

Other comparisons

Comparing leaping distances across years, seasons, and forest types shows few differences (Fig. 4). Overall, leaps up to 2 body lengths, about 1 m, represent approximately 80% of all leaps within all ecological contexts. The one exception to this is the wet season (1990), where longer leaps occurred more frequently (Fig. 4). The linear distances covered when leaping in the context of travel exhibited the same trends as the overall pattern (Fig. 4).

Rare or infrequent locomotor behaviors also vary by situation. In the wet season and in secondary forest, bimanualism, 3% and 2%, respectively, and vertical bounding, 4% and 3%, predominate among the less fre-

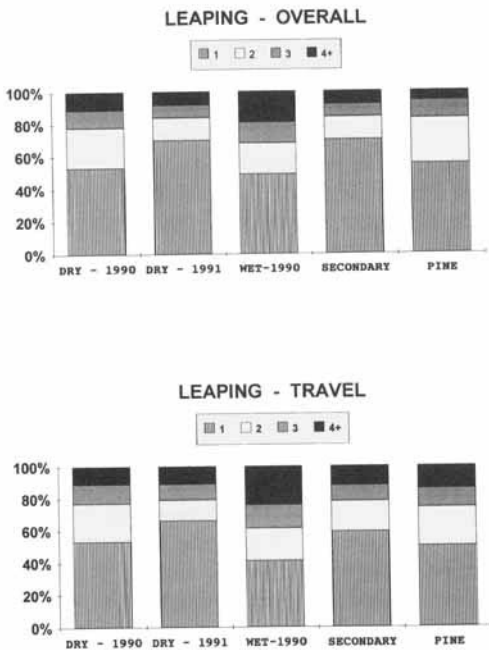


Fig. 4. Leaping distances in body lengths for travel and feeding combined (overall) and for travel. Horizontal or linear leaping distances are documented in *Colobus badius* for each type of forest, by year and by season. The mean body length for *Colobus badius* is 533 cm (Napier and Napier, 1967), thus a two-body length leap represents about 1 m in linear distance.

quent varieties of locomotion. In the pine plantation, vertical bounding is a low 1%, while bimanualism is 6%.

Few differences were recorded in postural behavior across ecological contexts (Table 5). In the dry season, the annual comparisons for the primary forest show postural frequencies to be virtually identical, as are the frequencies recorded during the wet season. Standing increases a few percent during the wet relative to the dry season (Table 5). In secondary and pine forests, sitting decreases in frequency and standing increases relative to their usage in primary forest. In secondary forest, bimanual suspension (3%) increases substantially relative to the other forests (<1%, Table 5).

DISCUSSION

Gebbo and Chapman (1994) described the locomotor and postural behavior of red colobus monkeys from data collected in primary

forest and compared this information to four other Old World monkeys. We noted that *Colobus badius* frequently uses arboreal quadrupedalism, leaping, and climbing in approximately equal amounts, while sitting is the predominate posture. Examining positional behavior in different ecological contexts does not change this overall assessment. Common positional behaviors are still common and rare behaviors occur infrequently across these comparisons. On the other hand, the frequencies for any single type of positional behavior, especially the more common varieties, change in each of our different ecological situations and activities. In fact, the activity feeding shows the highest magnitude of change relative to our annual, seasonal, or forest comparisons. Thus, species-specific locomotor frequencies, especially for common movements like quadrupedalism, climbing, and leaping, are much more variable than we had anticipated for red colobus monkeys. In conclusion, individual species show much greater flexibility in their behavioral profiles in relation to habitat modifications than we would have predicted.

What are the implications of this information for future assessments of primate positional behavior? First, our data suggest that common behaviors remain common, and thus, radical changes in positional behavior do not occur in different ecological contexts. This is important for our assessment of a species' locomotor identity since each species should be expected, within limits, to be "constrained" by anatomical design. For example, red colobus monkeys never utilize brachiation, although they are moderate users of bimanualism, nor does this change by season, year, or forest. Thus, positional behavior reflects anatomy, although this match may be less deterministic than many might prefer to acknowledge.

Second, although common behaviors are common across different ecological contexts, they do vary in their use by season, year, or forest type. Clearly, primates are more flexible in their behavioral adjustments to different ecological settings than previous work has documented. If we had reported only our data for feeding during the primary-forest wet season (1990), *Colobus ba-*

TABLE 5. *Red colobus* postural behavior in annual, seasonal, and forest type comparisons

| | Primary forest | | | Pines | Secondary | Range |
|------------------|----------------|----------|----------|-------|-----------|-------|
| | Wet 1990 | Dry 1990 | Dry 1991 | | | |
| Bouts | 1,086 | 2,566 | 1,685 | 1,266 | 1,348 | |
| Sit | 89% | 90% | 90% | 85% | 83% | 7 |
| Vertical cling | <1 | <1 | <1 | 2 | <1 | 1 |
| Hindlimb suspend | 0 | 0 | 0 | <1 | 0 | <1 |
| Bimanual suspend | 0 | <1 | 0 | <1 | 3 | 3 |
| Stand | 10 | 8 | 7 | 12 | 12 | 5 |
| Bipedal stand | <1 | 1 | 2 | 2 | 1 | 1 |
| Recline | <1 | 1 | <1 | <1 | 1 | <1 |

dius would be viewed as a frequent climber (48% of the time), while data from the dry season in the same forest (across years) and year (across forests) mark *Colobus badius* as a quadrupedal leaper (44% and 37%, respectively). Variation in positional behavior between the ecological contexts studied here indicates the need to ensure that the sample size obtained, the duration (type of season), and the number of habitats sampled are suitable to address the theoretical questions of interest. Future studies should consider the value of increased sampling, studies of longer duration, or repeat trips to the field to sample more seasons or contexts.

The third implication might be that primate species are capable of making choices in how they move through their environment according to their size, anatomy, food, and risk of predation (Avis, 1962; Prost and Sussman, 1969; Stern and Oxnard, 1973; Rose, 1974; Dykyj, 1980; Fleagle and Mittermeier, 1980, 1981; Grand, 1984; Fleagle, 1985; Roberts and Cunningham, 1986; Menzel, 1986; Boinski, 1989; Rodman, 1991; Cant, 1992; Dagosto, 1992; Garber, 1992), and that some of these conditions may change. Lastly, how can morphologists or paleontologists incorporate behavioral flexibility into their evolutionary studies of postcranial anatomy, limb function, and mechanical design? Ecobehavioral flexibility blurs our traditionally stereotypic assessments of primate locomotor potential. This flexibility adds to our general uncertainty concerning the locomotor identity or categorization of primate species, especially extinct species. Therefore, traditional locomotor assessments may not accurately reflect overall positional behavior and may incorrectly link anatomical form with a particu-

lar behavior. We advocate that increased effort must be placed on studying positional behavior to help minimize this problem. Until we are more fully able to unify our behavioral, ecological, anatomical, and historical work into a better predictive model for the study of positional behavior in primates, our assessments of primate locomotor adaptation and evolution will be limited. We believe that a renewed emphasis should be placed on collecting field data on an array of taxonomically diverse and different-sized primates, in a variety of different ecological contexts, to help resolve these issues and to hasten the development of better predictive models.

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