

Implications of Small Scale Variation in Ecological Conditions for the Diet and Density of Red Colobus Monkeys

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ABSTRACT. In this 3-year investigation we documented patterns of density, diet, and activity of red colobus monkeys (*Procolobus tephrosceles*) in six areas in or near Kibale National Park, Uganda and related these patterns to availability of food resources. There were large differences in the density and behavior of the red colobus among the sites. For example, the red colobus at one site with a diverse plant community of more than 61 tree species, had a diet that included at least 42 species. In contrast, at a second site red colobus spent 92% of their feeding time eating from one species that dominated the tree community. The density of important red colobus food trees varied among sites from 32 trees/ha to 204 trees/ha, and red colobus density ranged from 0.70 groups/km² to 7.41 groups/km². Among sites, red colobus density was related to the cumulative DBH of important food trees, when one apparently anomalous site was excluded, and populations with more plant species in their diets tended to be those that were found at higher densities. Activity budgets of the red colobus populations varied markedly among sites. For example, feeding time ranged among sites from 29 to 55%, and traveling varied from 5 to 20%. When faced with increased foraging demands, red colobus reduced the time spent resting, while the time spent socializing remained fairly constant. Comparative socioecological studies typically contrast species separated by large geographical distances to ensure there is sufficient variation in the environment to detect behavioral responses. The marked differences in ecological conditions and red colobus behavior we documented over short geographical distances, suggests that small-scale contrasts are a useful tool to examine ecological determinants of behavior and community structure.

Key Words: *Procolobus tephrosceles*; Population regulation; Kibale National Park; Foraging; Community structure; Activity budgets.

INTRODUCTION

Environmental factors are viewed to have pervasive effects on primate behavior and social organization (CROOK, 1970; ALTMANN & ALTMANN, 1970; KUMMER, 1971; WRANGHAM et al., 1993), and are believed to be key factors determining the richness of primate communities and the abundance of particular species (BOURLIÈRE, 1985; OATES et al., 1990; DAVIES, 1994; REED & FLEAGLE, 1995). The broad question that emerges from these studies is to what extent can primate behavior, species richness, and abundance be modeled as responses to varying ecological conditions?

Ecological studies that examine the functional significance of specific behavioral characters are typically polarized in that they involve either quantification of fine-grained variability, such as daily behavioral decisions made by individuals (WAGNER & ALTMANN, 1973; ALTMANN, 1974; RAEMAEKERS, 1980; POST, 1981), or course-grained comparative contrasts. The latter are often based on contrasts of independent studies conducted on populations or species that are separated by thousands of kilometers (EISENBERG et al., 1972; CLUTTON-BROCK & HARVEY, 1977; MCKEY, 1978; OATES et al., 1990; CHAPMAN et al., 1995). With regard to understanding how ecological conditions influence the abundance of particular species or the number of

primates species in a community, investigations almost universally make contrasts between sites that are widely separated (McKEY, 1978; McKEY et al., 1981; OATES et al., 1990; GANZHORN, 1992; KAY et al., 1997). The premise for contrasting widely separated populations is that sufficient variation will exist in ecological conditions among distant sites to permit detection of differences in response variables. However, if significant differences in ecological conditions occur over shorter distances, small-scale contrasts may be more sensitive at detecting ecological determinants than comparisons made on larger scales. At small spatial scales, phylogeny is controlled for, since contrasts can be made within a species, and un-measured ecological parameters (e.g. composition of the predator community) are less likely to differ among neighboring populations than would be the case among widely separated populations (BUTYNSKI, 1990; CHAPMAN & FEDIGAN, 1990). To date researchers employing a small-scale approach have tended to use seasonal comparisons of ecological conditions and behavior (GAUTIER-HION, 1980; RAEMAEEKERS, 1980; CHAPMAN, 1988), but there are other scales on which comparisons can be made (e.g. BUTYNSKI, 1990; CHAPMAN et al., 1995; BRONIKOWSKI & ALTMANN, 1996; STRUHSAKER, 1997). Studies examining neighboring sites within the same habitat (a small spatial scale: BUTYNSKI, 1990; CHAPMAN & FEDIGAN, 1990) or groups within one site over a long period of time (an expanded temporal scale: BRONIKOWSKI & ALTMANN, 1996) have found large differences in behavior or in the abundance of particular species. These few investigations suggest that, studies of ecological determinants of primate behavior and abundance may benefit by investigations conducted at small spatial scales.

The objective of this 3-year investigation is to document patterns of density, diet, and activity among red colobus (*Procolobus tephrosceles*) populations inhabiting six areas of Kibale National Park, Uganda. We related these patterns to the ecological conditions at each of the sites. The fact that these six areas are no more than 15 km apart permits an examination of the value of using small-scale contrasts to assess ecological determinants of red colobus density and behavior.

METHODS

STUDY SITES

Kibale National Park is located in western Uganda ($0^{\circ}13' - 0^{\circ}41' \text{ N}$ and $30^{\circ}19' - 30^{\circ}32' \text{ E}$) near the foothills of the Ruwenzori Mountains and contains moist evergreen forest (WING & BUSS, 1970; STRUHSAKER, 1975; SKORUPA, 1988; BUTYNSKI, 1990) (Fig. 1). Mean annual rainfall in the region (measured at Makerere University Biological Field Station, Kanyawara, Fig. 1) is 1,700 mm (1990–1996); the mean daily minimum temperature is 15.5°C ; and the mean daily maximum temperature is 23.7°C (1990–1996, CHAPMAN & CHAPMAN, unpubl. data). This study was conducted primarily at six sites distributed throughout the park or near the park (Sebatoli, Kanyawara K-30, Kanyawara K-15, Dura River, Mainaro, and Kahunge, Fig. 1), with additional comparisons made with a seventh site (Ngogo, CHAPMAN & CHAPMAN, 1997; CHAPMAN et al., 1997; STRUHSAKER, 1997).

Kibale forest received National Park status in 1993. Prior to 1993, it was a Forest Reserve, gazetted in 1932, with the stated goal of providing a sustained production of hardwood timber (OSMASTON, 1959). A polycyclic felling cycle of 70 years was initiated, and it was recommended that logging open the canopy by approximately 50% through the harvest of trees over 1.52 m in girth (KINGSTON, 1967). This history of logging has led to varying degrees of disturbance among sites. At Kanyawara (elevation 1,500 m) the K-15 forestry compartment is a 360-ha section of forest that experienced heavy selective felling in 1968 and 1969. Total harvest

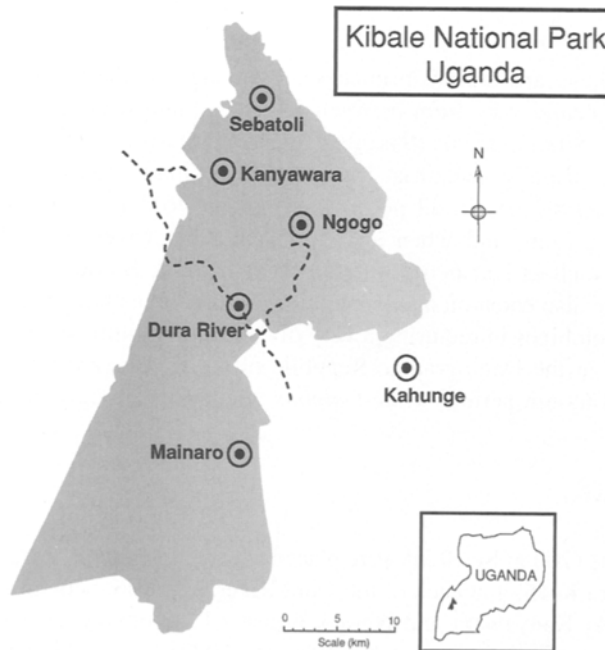


Fig. 1. A map of Kibale National Park, Uganda showing the location of the six study sites and the position of Kibale within Uganda.

averaged 21 m³/ha or approximately 7.4 stems/ha (SKORUPA, 1988); however incidental damage was much higher. A total of 18 tree species were harvested (14 of these species are known to be food sources for red colobus), with nine species contributing more than 95% of the harvest volume (of these nine, all were red colobus food trees: KASENENE, 1987; SKORUPA, 1988). Sebatoli (elevation 1,500 m) has also been logged, but we were unable to obtain information on the level of extraction. Detailed quantification of stand structure suggests that the level of extraction was similar to or slightly lower than that of K-15 (CHAPMAN & CHAPMAN, unpubl. data). K-30 is a 300-ha area that has not been commercially harvested but, prior to 1970, a few large stems (0.03 to 0.04 trees/ha) were removed by pitsawyers. This extremely low level of extraction seems to have had very little impact on the structure and composition of the forest (SKORUPA, 1988; STRUHSAKER, 1997). Similarly at Dura River (elevation 1,250 m) and Mainaro (elevation 1,200 m) a few timber trees have been extracted by pitsawyers (approximately 0.1 trees/ha), but this has had little impact on the forest.

Kahunge (elevation 1,220 m) represents a more seriously degraded site. It is outside of the park's boundary. As a result, the remaining forest has been reduced to a thin strip along the banks of the Mpanga River. Topographic maps from 1959 depict a similar level of forest cover, suggesting that the area has been degraded for several decades. Young trees within this riverine forest are often felled for fuelwood. All sites, except Kahunge, consist of a series of moderately undulating hills and valleys, and there are elevational changes from hill tops to valley bottoms of 150–200 m (measured with a Pauling Micro Surveying Altimeter).

STRUHSAKER (1997) provides density estimates of red colobus from Ngogo. Since we have collected comparable ecological data from Ngogo (CHAPMAN et al., 1997), it is included in our analyses relating food availability to red colobus density. This site (elevation=1,350 m) has not been impacted by logging.

STUDY ANIMAL

Red colobus monkeys are diurnal primates and throughout their range they are found in social groups that typically vary from between 25 and 40 monkeys, but group size can range from 3 to greater than 80 individuals (STRUHSAKER, 1975; OATES, 1994; CHAPMAN & CHAPMAN, unpubl. data). Groups usually contain at least three adult males and many adult females, and females are the dispersing sex. In all populations studied to date, young leaves are the most commonly eaten food item, and when animals eat mature leaves they often select specific sections of the leaf, such as leaf petioles (STRUHSAKER, 1975; BARANGA, 1982; OATES, 1994). Fruits and flowers are also eaten on a seasonal basis. Red colobus have been suggested to differ from other African colobines in requiring a very diverse diet (STRUHSAKER & OATES, 1975). For example, at Salonga in the Democratic Republic of the Congo, red colobus ate 80 different plant species in an 8-month period, while *Colobus angolensis* ate only 46 species (MAISELS et al., 1994).

VEGETATION MONITORING

Vegetation transects (200 m by 10 m) were placed at each study site (12 transects at Kanyawara K-30; 5 at Kanyawara K-15; 4 at each of the Dura River, Mainaro, Sebatoli, and Kahunge sites; and 24 at Ngogo). At Kanyawara and Ngogo, transect location was selected at random from within existing trail systems (CHAPMAN & CHAPMAN, 1997). At the Mainaro, Dura River, and Sebatoli sites there were no preexisting trails, and transects were established perpendicular to each other at 50- to 100-m intervals. At Kahunge, transects were placed parallel to the river, because the forest was limited to this thin riverine strip. This regime produced a total sampling area of 11.4 ha (2.4 ha at Kanyawara K-30; 1 ha Kanyawara K-15; 0.8 ha at Dura River, Mainaro, Sebatoli, and Kahunge; and 4.8 ha at Ngogo). Each tree greater than 10 cm DBH (Diameter at Breast Height) within 5 m of each side of the trail was individually marked with a numbered aluminum tag and measured (DBH). This produced a sample of 5,054 trees (1,173 trees at Kanyawara K-30; 244 at Kanyawara K-15; 338 at Dura River; 293 at Mainaro; 322 at Sebatoli; 62 at Kahunge; and 2,622 at Ngogo).

Phenological information has been recorded continuously once a month between January 1990 and July 1997 at Kanyawara ($n=91$ months); July 1995 and July 1997 at both Mainaro and Dura River ($n=24$ months); July 1996 and July 1997 at Sebatoli ($n=12$ months); and May 1990 and March 1997 at Ngogo ($n=86$ months). The stage of leaf development was documented (leaf bud, young leaves, mature leaves: visually assessed through binoculars), and we noted the presence or absence of flowers and ripe and unripe fruits for all trees.

BEHAVIORAL OBSERVATIONS

To quantify diet and activity of red colobus, we used a scan method that closely approximates the methods used in a number of previous studies in Kibale (WASER, 1974; STRUHSAKER, 1975; BUTYNSKI, 1990). Observations were made from July 1994 to July 1997 at Kanyawara, from July 1996 to June 1997 at Sebatoli, Dura River, and Mainaro, and from July 1995 to June 1996 at Kahunge, producing 1,177 hours of observation. In each half hour that the observer was with the group, five scans were made of different individuals that were in clear view. For each scan, the first activity the individual sustained for at least five continuous seconds was noted. If the animal was feeding, the species and the plant part (e.g. fruit, young leaf, leaf petiole) were recorded. We limited observations to adults, since we were primarily interested in foraging, and

we were not attempting to understand ontogenetic changes in feeding patterns. When possible, observations were made at each location during two consecutive days each month. Since Kahunge was very difficult to access, observations were only made during one day a month. On the first day, an attempt was made to locate the study group early in the morning and follow it until late afternoon. This assisted in locating the same group the next morning. Observations generally began at 08:30 and ended at 16:00; however there was variation in the time that observations started because of difficulties in traveling to sites or because the study group could not be readily located. To address this potential bias, behavioral samples from different sites were adjusted so that the same proportion of observations were made in each hour of the day. This was done by randomly removing observations from the data sets of sites with the greater number of observation hours during a particular hour of the day. This approach produces a sample that can be compared among sites; however caution must be used when comparing the results of this study to sampling conducted using different methods.

These behavioral observations were used to determine which tree species were important food sources for the red colobus of Kibale. The five tree species that were most frequently recorded to be eaten in the scans at any of the six sites were defined as "important food sources." Feeding on these food trees entailed an average of 75% of the foraging scans. The cumulative DBH of these species per ha was used as an index of food availability. To obtain an index of dietary richness for the populations, 167 foraging bouts (the smallest sample for any one site) were randomly selected from each population's scan data, and the number of food species consumed was calculated. This provides a measure of dietary richness that is not influenced by the fact that different populations were observed for different periods.

Variability in activity budgets was assessed using the Coefficient of Variation (CV, standard deviation in the percentage of scans involving a particular activity among sites divided by the mean: LEHNER, 1996). This is an appropriate measure to employ since we wish to assess how variable an activity was among populations regardless of how frequently that behavior was expressed. For example, one might wish to ask was there more variation in a commonly occurring activity, like feeding, than a relatively less commonly occurring behavior, like grooming. Significant differences among CVs were determined using the *C*-test statistic (DAWKINS & DAWKINS, 1973; LEHNER, 1996).

CENSUS

At each of the sites (except Kahunge) a 4-km census route was established to estimate the density of primate groups. The census was conducted following the line-transect procedures previously used in Kibale (STRUHSAKER, 1975; NATIONAL RESEARCH COUNCIL, 1981; SKORUPA, 1988; & BUTYNSKI, 1990). Observers walked slowly (approximately 0.8 km/hr) and stopped every 30 to 60 m for 30–60 sec to look and listen. When a monkey species was seen, the perpendicular distance to the first animal seen and the distance from the observer to the animal was visually estimated and the species determined. Starting in June 1996, these data were collected biweekly at K-30 ($n=26$), K-15 ($n=24$), and Dura ($n=23$) and once a month at Sebatoli ($n=14$) and Mainaro ($n=10$). Rebel activity prevented us from sampling at Mainaro in January, February, and April 1997.

There are a variety of methods proposed for estimating primate density using line-transect data and considerable controversy regarding the accuracy of different approaches (BURNHAM et al., 1980; CHAPMAN et al., 1988; SKORUPA, 1988; STRUHSAKER, 1997). Given this controversy and the difficulty of obtaining the needed sample size to use computer programs such as "Distance" (BUCKLAND et al., 1993), it is probably safest to rely on empirical criteria for

selecting the best methodology. GHIGLIERI (1979, 1984), STRUHSAKER (NATIONAL RESEARCH COUNCIL, 1981), and SKORUPA (1988) concluded that a modified KELKER (1945) method produced the best empirical results for primates in Kibale. Following these recommendations, we pooled data from census areas where the distance from the observer to the animal did not differ (ANOVA) and plotted the distance at 10-m intervals. This permitted us to estimate the observer to animal distance for each species. Subsequently, we selected the observer to animal distance to a 50% cut-off-rule. If X_i is the number of sightings in observer to animal distance class i for a given species, the last distance considered was at the end of the first class such that X_{i+1}/X_i and X_{i+2}/X_i were both equal to 0.50 or less. We used the observer to animal distance rather than perpendicular distance, because empirical data indicate that perpendicular distance underestimates transect width (NATIONAL RESEARCH COUNCIL, 1981; WHITESIDES et al., 1988; CHAPMAN et al., 1988). Finally, we corrected for the fact that animals on the periphery of a group are the ones most likely to be sighted first, but one really wishes to estimate the distance to the geometric center of the group (BURNHAM et al., 1980; SKORUPA, 1988). To compensate for this bias, we assumed that the dispersion of a group is circular and estimated the difference between peripheral and central sighting distance as one-half group spread (r : group spread values follow SKORUPA, 1988). Thus, the density of groups was estimated using the following formula: $D=(G_T)/L(2T+r)$, where G_T =the number of groups sighted within the truncated observer to animal distance, T =the truncated observer to animal distance, L =the length of the census route, and r =the average group radius. Since Kahunge represented a small riverine strip of forest it was possible to repeatedly sample the entire area to determine absolute red colobus group density. STRUHSAKER (1997, pers. comm.) present criticism of using sighting distance methods to estimate primate density. Thus, it might be more appropriate to consider the estimates that we derive from this approach as a relative measure, rather than as absolute density.

At the beginning of the study observers trained together to estimate observer to animal distance. At the end of study the variation between observers in sighting estimates was assessed. While particular estimates could be inaccurate, overestimates of distances tended to be countered by underestimates.

RESULTS

FOOD RESOURCE POTENTIAL

Six of the sites were closed canopy forest; four of these were relatively undisturbed by human activity, while two sites had been commercially logged. Logging removed a number of red colobus food trees, caused a large amount of incidental damage, and created gaps in the canopy that are difficult for animals to traverse. These impacts to forest structure are evident even 30 years post logging (STRUHSAKER, 1997; CHAPMAN & CHAPMAN, 1997). The seventh site differed considerably from the other sites: Kahunge is an area outside of the park and entails a thin strip of riverine forest that is dominated by *Acacia kirkii*.

Densities of many tree species differed markedly among sites (Table 1). For example, two of the ten most common trees at Ngogo (*Dictyandra arborescens* and *Pterygota mildbraedii*) were very rare at Kanyawara (*Pterygota mildbraedii* occurs in K-30 but was not recorded on the transects). *Baphiopsis parviflora* and *Cynometra alexandri* were the most abundant tree species at Mainaro, but were not found at the other locations. *Bequaertidendron oblanceolatum* was the third most common species at Dura River, but was not found on the transects at any other location. *Uvariopsis congensis*, which was either the most abundant or the second most abundant

Table 1. The density of trees (individuals/ha) found at seven sites in Kibale National Park, Uganda.

Species	Sebatoli	K-15	K-30	Ngogo	Dura River	Mainaro	Kahunge
<i>Uvariopsis congensis</i>	—	3.0	60.4	100.6	60.0	43.8	—
<i>Celtis durandii</i>	2.5	33.0	47.1	57.5	63.8	33.8	—
<i>Funtumia latifolia</i>	25.0	27.0	33.8	36.3	43.8	2.5	—
<i>Diospyros abyssinica</i>	2.5	54.0	40.0	69.0	1.3	1.3	—
<i>Markhamia platycalyx</i>	38.8	43.0	50.0	24.8	8.8	1.3	—
<i>Chrysophyllum</i> sp.	8.8	1.0	2.6	64.6	47.5	21.2	—
<i>Baphiopsis parviflora</i>	—	—	—	—	—	116.3	—
<i>Tabemaemontana</i> sp.	28.8	2.0	4.6	34.4	8.8	—	—
<i>Bosqueia phoberos</i>	—	—	50.0	5.6	22.5	—	—
<i>Cynometra alexandri</i>	—	—	—	—	—	63.8	—
<i>Bequaertiodendron oblancoelatum</i>	—	—	—	—	57.5	—	—
<i>Strombosia scheffleri</i>	36.3	1.0	12.5	3.1	2.5	—	—
<i>Croton</i> sp.	41.3	4.0	0.8	0.4	—	1.3	—
<i>Leptonychia mildbraedii</i>	—	—	35.4	2.5	—	—	—
<i>Celtis mildbraedii</i>	—	—	—	0.2	—	32.5	—
<i>Newtonia buchananii</i>	26.3	1.0	—	0.2	3.8	—	—
<i>Aningeria altissima</i>	23.8	2.0	1.7	—	2.5	—	—
<i>Myrianthus arboreus</i>	16.3	10.0	2.1	—	—	—	—
<i>Pleiocarpa pycnantha</i>	6.3	3.0	1.3	1.3	13.8	2.5	—
<i>Chaetacme aristata</i>	—	1.0	17.1	4.8	3.8	1.3	—
<i>Neoboutonia</i> sp.	8.8	10.0	1.3	7.9	—	—	—
<i>Millettia dura</i>	3.8	8.0	3.3	7.7	1.3	—	2.0
<i>Cassipourea ruwensorensis</i>	2.5	9.0	7.1	5.0	—	—	—
<i>Linociera johnsonii</i>	8.8	1.0	5.4	7.5	—	—	—
<i>Xymalos monospora</i>	10.0	1.0	8.8	2.3	—	—	—
<i>Teclea nobilis</i>	—	1.0	17.1	3.8	—	—	—
<i>Mimusops bagshawei</i>	6.3	1.0	3.3	3.1	7.5	—	—
<i>Premna angolensis</i>	—	8.0	4.6	4.4	2.5	1.3	—
<i>Dictyandra arborescens</i>	—	—	0.4	12.1	3.8	3.8	—
<i>Acacia kirkii</i>	—	—	—	—	—	—	20.0
<i>Trema orientalis</i>	—	19.0	—	—	—	—	—
<i>Aphania senegalensis</i>	—	1.0	1.7	4.6	3.8	3.8	—
<i>Dasylepis</i> sp.	2.5	—	1.3	7.9	2.5	—	—
<i>Dombeya mukole</i>	—	—	9.2	3.1	1.3	—	—
<i>Celtis africana</i>	—	7.0	4.2	1.0	—	1.3	—
<i>Ficus mucoso</i>	—	—	—	0.6	1.3	11.3	—
<i>Turraeanthus africanus</i>	12.5	—	—	0.4	—	—	—
<i>Kigelia moosa</i>	3.8	5.0	3.3	0.8	—	—	—
<i>Lovoa swynnertonii</i>	3.8	—	0.8	4.4	3.8	—	—
<i>Albizia grandibracteata</i>	—	—	1.3	—	1.3	—	10.0
<i>Ehretia cymosa</i>	7.5	5.0	—	—	—	—	—
<i>Pancovia turbinata</i>	—	—	10.8	0.2	1.3	—	—
<i>Blighia unijugata</i>	7.5	2.0	0.8	1.0	—	—	1.0
<i>Cordia abyssinica</i>	6.3	6.0	—	—	—	—	—
<i>Pterygota mildbraedii</i>	—	—	—	10.8	1.3	—	—
<i>Maerua duchesnei</i>	—	10.0	1.3	0.4	—	—	—
<i>Fagaropsis angolensis</i>	6.3	2.0	2.5	0.6	—	—	—
<i>Alangium chinense</i>	10.0	—	—	—	—	—	—
<i>Rothmannia urcelliformis</i>	—	2.0	1.3	5.2	1.3	—	—
<i>Olea welwitschii</i>	—	2.0	3.3	3.1	1.3	—	—
<i>Ficus exasperata</i>	2.5	—	3.8	0.4	—	1.3	—
<i>Turraea</i> sp.	—	—	—	1.5	—	6.3	—
<i>Strychnos mitis</i>	—	—	7.5	0.2	—	—	—
<i>Harrisonia abyssinica</i>	—	—	—	2.5	2.5	2.5	—
<i>Polyscias fulva</i>	3.8	—	0.8	0.2	—	2.5	—
<i>Pseudospondias microcarpa</i>	—	—	1.7	1.3	3.8	—	—
<i>Cola gigantea</i>	—	—	—	—	6.3	—	—
<i>Ficus conraui</i>	2.5	3.0	0.4	0.2	—	—	—
<i>Monodora myristica</i>	—	—	0.4	0.4	3.8	1.3	—

(continued)

Table 1. (continued)

Species	Sebatoli	K-15	K-30	Ngogo	Dura River	Mainaro	Kahunge
<i>Ficus sansibarica</i>	—	2.0	1.7	2.1	—	—	—
<i>Zanthoxylum lepreurii</i>	3.8	1.0	0.8	0.2	—	—	—
<i>Prunus africana</i>	2.5	—	—	3.0	—	—	—
<i>Sapium ellipticum</i>	2.5	—	—	0.6	—	—	2.0
<i>Lychnodiscus cerospermus</i>	—	—	—	—	5.0	—	—
<i>Balanites wilsoniana</i>	—	—	1.7	1.7	1.3	—	—
<i>Tarenna pavettoides</i>	—	—	—	4.4	—	—	—
<i>Carapa grandiflora</i>	3.8	—	—	—	—	—	—
<i>Ritchiea albersii</i>	3.8	—	—	—	—	—	—
<i>Bersama abyssinica</i>	1.3	2.0	0.4	—	—	—	—
<i>Ficus sur</i>	1.3	1.0	—	—	—	1.3	—
<i>Parinari excelsa</i>	—	—	2.9	0.2	—	—	—
<i>Spathodea campanulata</i>	—	—	0.8	2.3	—	—	—
<i>Schrebera arborea</i>	—	—	—	1.5	1.3	—	—
<i>Cassine buchananii</i>	—	—	0.4	2.7	1.3	—	—
<i>Vitex amboniensis</i>	—	—	—	0.2	2.5	—	—
<i>Albizia glaberrima</i>	—	—	—	—	2.5	—	—
<i>Bombax buonopozense</i>	—	—	—	—	—	2.5	—
<i>Craiba brownii</i>	—	—	—	—	—	2.5	—
<i>Irvingia gabonensis</i>	2.5	—	—	—	—	—	—
<i>Suregada procera</i>	—	—	—	—	—	2.5	—
<i>Casearia</i> sp.	—	1.0	1.3	0.2	—	—	—
<i>Rauvolfia oxyphylla</i>	—	—	—	2.1	—	—	—
<i>Ficus cyathistipula</i>	—	1.0	—	1.0	—	—	—
<i>Piptadeniastrum africanum</i>	—	—	—	1.9	—	—	—
<i>Ficus saussureana</i>	—	—	—	0.6	—	1.3	—
<i>Margaritaria discoidea</i>	—	1.0	—	2.1	—	—	—
<i>Craterispermum laurinum</i>	—	—	1.7	—	—	—	—
<i>Treculia africana</i>	—	—	—	0.2	1.3	—	—
<i>Vangueria apiculata</i>	—	—	—	0.2	1.3	—	—
<i>Allophylus</i> sp.	—	—	—	—	—	1.3	—
<i>Alstonia boonei</i>	—	—	—	—	—	1.3	—
<i>Ficus vallis-choudae</i>	—	—	—	—	1.3	—	—
<i>Lindackeria</i> sp.	—	—	—	1.3	—	—	—
<i>Thecacoris lucida</i>	—	—	1.3	—	—	—	—
<i>Trichilia</i> sp.	1.3	—	—	—	—	—	—
<i>Warbugia ugandensis</i>	—	—	—	1.3	—	—	—
<i>Cleistanthus polystachyus</i>	1.3	—	—	—	—	—	—
<i>Euadenia eminens</i>	—	1.0	—	0.2	—	—	—
<i>Ficus natalensis</i>	—	—	0.4	0.6	—	—	—
<i>Apodytes dimidiata</i>	—	—	0.8	—	—	—	—
<i>Euclina longiflora</i>	—	—	0.8	—	—	—	—
<i>Cordia millenii</i>	—	—	0.4	0.2	—	—	—
<i>Ficus trichopoda</i>	—	—	—	0.4	—	—	—
<i>Macaranga schewinifurthii</i>	—	—	—	0.4	—	—	—
<i>Mitragyna rubrostipulata</i>	—	—	—	0.4	—	—	—
<i>Oncoba</i> sp.	—	—	—	0.4	—	—	—
<i>Oxyanthus latifolia</i>	—	—	—	0.4	—	—	—
<i>Antiaris toxicaria</i>	—	—	0.4	—	—	—	—
<i>Beilshmedia ugandensis</i>	—	—	0.4	—	—	—	—
<i>Coffea eugenoides</i>	—	—	0.4	—	—	—	—
<i>Symphonia globulifera</i>	—	—	0.4	—	—	—	—
<i>Entandrophragma angolense</i>	—	—	—	0.2	—	—	—
<i>Ficus ovata</i>	—	—	—	0.2	—	—	—
<i>Morus lactea</i>	—	—	—	0.2	—	—	—
<i>Psychotria</i> sp.	—	—	—	0.2	—	—	—
<i>Rinorea oblongifolia</i>	—	—	—	0.2	—	—	—

Species are listed in order of their overall abundance at all of the sites.

species at four of the sites, was rare in K-15 and absent from Sebatoli. *Acacia kirkii*, which was the most abundant tree at Kahunge and the species on which the red colobus there fed on the most, was not found at any of the other sites.

Using behavioral data to identify red colobus food sources, we examined variation in the nature of the food resources among sites and found a number of inter-site differences (Tables 2 & 3).

Table 2. The density (individuals/ha) of the preferred red colobus food trees (top five most eaten species at any of the sites) found at seven sites in Kibale National Park, Uganda.

Species	Sebatoli	K-15	K-30	Ngogo	Dura	Mainaro	Kahunge
<i>Celtis durandii</i>	2.5 ⁵	33.0 ¹	47.1 ²	57.5	63.8 ¹	33.8 ²	—
<i>Funtumia latifolia</i>	25.0 ⁵	27.0 ⁵	33.8	36.3	43.8 ³	2.5	—
<i>Markhamia platycalyx</i>	38.8	43.0 ³	50.0 ⁴	24.8	8.8	1.3	—
<i>Bosqueia phoberos</i>	—	—	50.0	5.6	22.5	— ⁴	—
<i>Cynometra alexandri</i>	—	—	—	—	—	63.8 ¹	—
<i>Strombosia scheffleri</i>	36.3 ²	1.0	12.5 ⁵	3.1	2.5	—	—
<i>Newtonia buchananii</i>	26.3 ¹	1.0	—	0.2	3.8	—	—
<i>Aningeria altissima</i>	23.8 ³	2.0 ⁴	1.7	—	2.5 ²	—	—
<i>Mimusops bagshawei</i>	6.3	1.0	3.3	3.1	7.5	— ⁴	—
<i>Acacia kirkii</i>	—	—	—	—	—	—	20.0 ¹
<i>Celtis africana</i>	—	7.0 ²	4.2 ³	1.0	—	1.3 ⁵	—
<i>Albizia grandibracteata</i>	—	—	1.3	—	1.3 ⁴	—	10.0 ²
<i>Blighia</i> sp.	7.5	2.0	0.8	1.0	1.3	—	—
<i>Cola gigantea</i>	—	—	—	—	6.3 ⁵	—	—
<i>Prunus africana</i>	2.5 ⁴	—	— ¹	3.0	—	—	—
<i>Sapium ellipticum</i>	2.5	—	—	0.6	—	—	2.0 ²
Total density	171.3	117.0	204.0	136.3	164.0	102.7	32.0
Cumulative DBH	9496	2759	5548	3911	6708	4747	1765.0

The superscripts indicate the ranking of the five most commonly eaten species is provided for sites where behavioral data were collected.

Table 3. The percentage of foraging scans involving the top five most frequently eaten plant species (underlined) at each of six sites in Kibale National Park, Uganda and the corresponding use at the other sites.

Species	Sebatoli	K-15	K-30	Dura	Mainaro	Kahunge
<i>Acacia kirkii</i>	—	—	—	—	—	<u>91.9</u>
<i>Celtis durandii</i>	<u>5.4</u>	<u>23.6</u>	<u>10.4</u>	<u>27.2</u>	6.0	—
<i>Cynometra alexandri</i>	—	—	—	—	<u>40.7</u>	—
<i>Funtumia latifolia</i>	<u>5.4</u>	<u>8.1</u>	7.2	<u>12.8</u>	3.0	—
<i>Aningeria altissima</i>	<u>8.7</u>	<u>8.7</u>	0.9	<u>14.9</u>	—	—
<i>Celtis africana</i>	4.3	<u>12.2</u>	<u>9.9</u>	1.5	—	—
<i>Albizia grandibracteata</i>	1.0	4.1	8.4	<u>10.8</u>	1.8	<u>0.7</u>
<i>Strombosia scheffleri</i>	<u>10.9</u>	0.9	<u>9.2</u>	2.7	—	—
<i>Markhamia platycalyx</i>	3.1	<u>10.2</u>	<u>9.2</u>	1.0	—	—
<i>Prunus africana</i>	<u>5.9</u>	1.7	<u>13.0</u>	—	2.4	—
<i>Bosqueia phoberos</i>	3.1	—	0.8	3.1	<u>5.4</u>	—
<i>Newtonia buchananii</i>	<u>11.2</u>	—	—	—	—	—
<i>Mimusops bagshawei</i>	0.8	—	0.4	4.6	<u>5.4</u>	—
<i>Celtis zenkeri</i>	—	—	—	—	<u>5.4</u>	—
<i>Cola gigantea</i>	—	—	—	<u>5.1</u>	—	—
<i>Sapium ellipticum</i>	1.3	—	0.1	—	0.6	<u>0.7</u>
<i>Bridelia micrantha</i>	—	—	1.6	—	—	<u>0.7</u>

Species are listed in order of their overall frequency of use at all of the sites. Only four plant species were eaten at Kahunge.

First, many important foods were only present at one or a limited number of the sites. Second, some populations relied heavily on one or a few tree species. The most apparent example of this involves the red colobus at Kahunge that ate *Acacia kirkii* for 92% of their feeding time. Similarly, *Cynometra alexandri* was eaten by the Mainaro population for 41% of that group's feeding time. Third, in some areas red colobus had very rich diets, while in other areas they did not. For example, the red colobus at Sebatoli had a diverse diet that included items from 27 tree species, while the red colobus at Kahunge were only seen eating from four tree species (dietary richness Kanyawara K-30: 22 species; Kanyawara K-15: 18 species; Dura River: 17 species; Mainaro: 24 species; based on the same sample size of foraging scans for each site).

The density of red colobus food trees varied from 32 trees/ha to 204 trees/ha. Evaluating the resource potential of the different areas more appropriately as the cumulative DBH of these food bearing trees produces different ranking of the areas, but large differences in the availability of food are still evident among sites (1,765 cm DBH/ha to 9,496 cm DBH/ha; Table 2). There was no relationship between the availability of food resources and the time that the groups spent feeding ($r_s = -0.543$, $p = 0.266$).

RED COLOBUS DENSITY

Red colobus density varied among the seven sites from 0.70 groups/km² to 7.41 groups/km² (Sebatoli: 6.38 groups/km²; Kanyawara K-30: 6.07 groups/km²; Kanyawara K-15: 3.24 groups/km²; Dura River: 0.70 groups/km²; Mainaro: 7.41 groups/km²; and Kahunge: 1.67 groups/km²). Group density was not related to the cumulative DBH of the important food sources ($r_s = 0.321$, $p = 0.241$, $n = 7$, Fig. 2A). However, examining the distribution of these points suggests that the Dura River population may have an unusually low red colobus density relative to the availability of food resources, in fact it has the lowest density of all sites, but it is an undisturbed forest site (Fig. 2A). If the Dura River site is excluded, the cumulative DBH of important food trees does predict red colobus group density ($r_s = 0.83$, $p = 0.021$). The populations that had richer diets tended to be those that were found at higher densities. This relation-

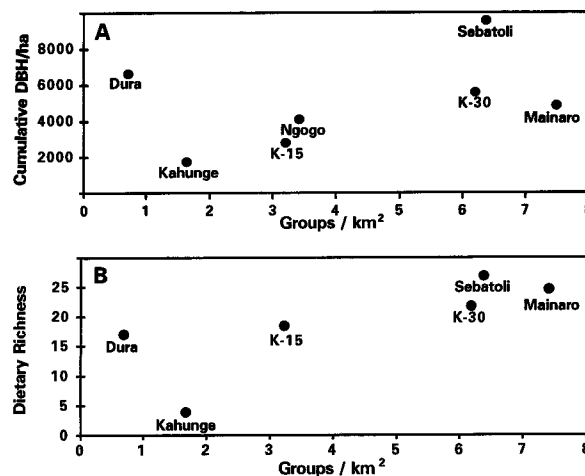


Fig. 2. A. The relationship with group density and the cumulative DBH of red colobus food trees among seven sites in Kibale National Park, Uganda; B. the relationship with group density and the dietary richness for six populations of red colobus found in Kibale National Park, Uganda.

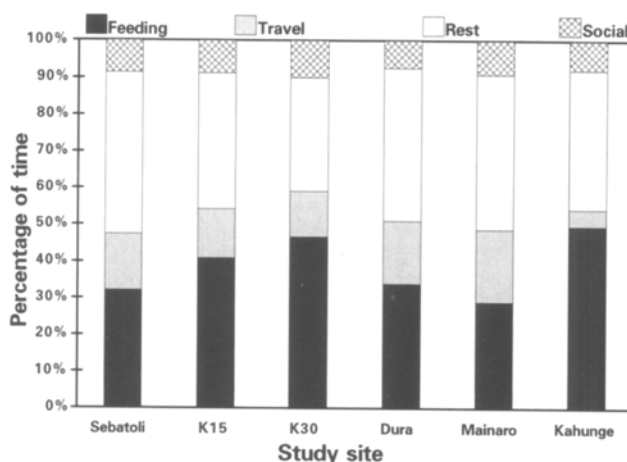


Fig. 3. The activity budgets of red colobus groups found at six sites in or near Kibale National Park, Uganda.

ship held whether the Dura River site was included ($r_s=0.886$, $p=0.009$, $n=7$) or excluded ($r_s=0.900$, $p=0.019$, $n=6$, Fig. 2B).

SPATIAL VARIATION IN RED COLOBUS BEHAVIOR

The amount of time the red colobus spent feeding ranged from 49.7% at Kahunge to 29% at Mainaro (Fig. 3). The proportion of the scans that involved traveling varied among areas from 4.6% at Kahunge to 19.8% at Mainaro. At Mainaro, it was evident that when the red colobus were not feeding on *Cynometra alexandri*, they had to travel long distances among feeding sites, because food trees were widely dispersed within the monodominant *Cynometra* stand. At Kahunge the animals were feeding primarily (92%) on *Acacia kirkii*, the most abundant tree at the site. This produced very short travel distances among food trees.

Activity budgets can be used to assess if there is an ideal or minimum tolerable time for various activities. ALTMANN (1980) proposed that when social groups are faced with increased foraging demands, they should reduce the amount of time devoted to socializing, rather than reducing resting time. With the red colobus of Kibale, resting was more variable among the six populations than was socializing (CV, resting: 12.5; socializing: 10.7, $t=8.00$, $p<0.001$). Furthermore, the combined activities of feeding and traveling were negatively correlated to resting ($r_s=-0.986$, $p<0.01$), but they were not related to the time spent socializing ($r_s=0.319$, $p=0.538$).

The red colobus at the different sites relied on different plant parts to differing degrees (Table 4). At all sites, young leaves were the most frequently eaten plant part; however, some populations relied heavily on fruit (typically unripe) or flowers, while others did not. This degree of dietary flexibility does not change our impression that red colobus are folivores, but it does change our impression of how much they can rely on mature leaves or use flowers or fruit (Table 4).

DISCUSSION

This study documented large differences in the density of red colobus monkey groups among areas in or near Kibale National Park that are separated by less than 15 km. Furthermore, groups

Table 4. Dietary components from red colobus groups from six areas in Kibale National Park, Uganda.

Location	Young leaves	Mature leaves	Leaf petiole	Fruit	Flowers	Bark
Sebatoli	72.4	7.4	7.1	6.4	3.3	2.0
K-15	69.8	2.6	5.8	17.2	2.3	0.3
K-30	57.6	9.9	14.2	6.7	2.0	4.1
Dura River	65.1	4.6	8.7	13.9	6.2	0.0
Mainaro	57.5	16.2	1.8	10.8	7.2	3.6
Kahunge	48.8	21.0	0.0	3.1	22.7	2.7
Largest difference	23.6	18.4	14.2	14.1	20.7	3.6

The components do not sum to 100% because of groups eating plant parts that are not listed (e.g. the K-30 groups at 3.0% pine needles).

in these different areas were found to have markedly different diets and activity budgets. These findings can be interpreted with regard to three issues: ecological determinants of red colobus abundance, optimal allocation of time in activity budgets, and the value of comparative studies on different scales.

ECOLOGICAL DETERMINANTS OF RED COLOBUS ABUNDANCE

What insights do our data provide to understanding the abundance of red colobus? If one is willing to accept the possibility that the Dura River population is presently at an anomalously low density, then an argument can be made that red colobus density is influenced by food availability.

Is it appropriate to exclude the Dura River site? There are a number of reasons to believe that the red colobus population at the Dura is not at carrying capacity. First, STRUHSAKER (1975) conducted five censuses at the Dura River between October 1970 and March 1971, each 4.5 km in length (the census route was not identical to the one we used). These earlier censuses estimated red colobus group density at 1.9 groups/km², a density 2.7 times greater than we recorded. This suggests that this population may have been reduced below carrying capacity in recent history. Second, STRUHSAKER (pers. comm.) describes an epidemic that killed a number of male red colobus at Ngogo in the early 1980s. If such epidemics are common and are restricted to one or a few sites, they could reduce populations periodically to levels below carrying capacity.

In general, there is only scant evidence that disease and parasites regulate primate population size (FREELAND, 1977; ANDERSON & MAY, 1979; SCOTT, 1988); however they can clearly cause short-term reductions in population size. A yellow fever epidemic was implicated in a 50% population decrease of howler monkeys (*Alouatta palliata*) on Barro Colorado Island, Panama between 1933 and 1951 (COLLIAS & SOUTHWICK, 1952). However, within eight years the population reached a size higher than that before the outbreak. The effects of parasite load has also been studied on the howler monkeys of Barro Colorado Island (MILTON, 1996). MILTON (1996) found that the relative density of bot-fly infestations on the howlers was positively correlated with howler mortality. She concluded that howler mortality is often due to the combined factors of physical condition, degree of bot-fly infestation, and dietary stress.

Our data suggest that areas with higher red colobus food abundance support more red colobus (significant only after excluding the Dura River site) than sites where less food is available. It is possible to assess the generality of this relationship by examining sites at which the food supply has changed over time. With respect to studies of other red colobus populations, a combination of natural and human-induced disturbance have been implicated in the decline of the red

colobus (*Procolobus rufomitratu*s) at Tana River, Kenya (DECKER, 1989). This population declined by approximately 80% between 1975 and 1985 (MARSH, 1986). DECKER (1989) attributes this decline to loss and fragmentation of habitat due mostly to clearcutting of forest for agriculture in the 1960s. She suggests that the high population densities reported in 1975 reflect a population well above its carrying capacity, while the subsequent censuses in the 80s reflect a population adjusted to the new constraints of the habitat. The observation that red colobus in the 1975 study were eating a higher proportion of mature leaves than red colobus a decade later suggests that loss of food resources was the mechanism regulating population density (DECKER, 1989).

There are a number of similar examples involving long-lasting declines in resource availability and declines in primate populations. For example, vervet populations (*Cercopithecus aethiops*) in Amboseli, Kenya (STRUHSAKER, 1973, 1976) declined by 43% between 1964 and 1975 with a natural reduction in their food resources. Similar examples are evident with baboons (*Papio anubis*) in Amboseli (ALTMANN et al., 1977) and toque macaques (*Macaca sinica*) in Sri Lanka (DITTS, 1977).

Short-term reductions in food availability can also impact primate populations (MILTON, 1990). One example is the failed fruit crop of 1970 on Barro Colorado Island, which led to a widespread famine and decline of frugivore populations (FOSTER, 1982). However, the population of howler monkeys soon recovered (MILTON, 1982), indicating that a failed fruit crop in a single year does not regulate populations over the long-term. This example also indicates that superannual periods of fruit scarcity, described by WEINS (1977) and CANT (1980) as ecological crunches, may not have a long-term regulating influence.

Our data suggest that red colobus abundance is not only influenced by the availability of food, but also by the nature of the available foods. In Kibale, areas with richer red colobus diets were characterized by higher red colobus densities. STRUHSAKER and OATES (1975) suggested that red colobus differ from other colobines, specifically black-and-white colobus (*Colobus guereza*), in that they require a very diverse diet. Their apparent need for a diverse diet may be the result of processes operating on two temporal scales. On a short time scale, these animals may need to eat a variety of plant species to meet their nutritional requirements. This is supported by the fact that red colobus tend to eat from a number of different tree species in a single day (STRUHSAKER, 1975). On a longer temporal scale, red colobus in areas that offer a more diverse suite of tree foods species may provide more foraging options during periods of food scarcity than animals in less diverse areas.

Food quality may also be a critical parameter impacting the density and foraging ecology of red colobus. While not considered by this study to date, several studies have found a positive relationship between food quality and folivorous primate biomass. Asian and African colobine biomass is positively related to an index of leaf quality, the ratio of protein to fiber (DAVIES, 1994; OATES et al., 1990; WATERMAN et al., 1988). A similar relationship was found between leaf quality and the biomass of folivorous lemurs of Madagascar (GANZHORN, 1992).

OPTIMAL ALLOCATION OF TIME IN ACTIVITY BUDGETS

Since activity budgets varied among our study groups, we can explore if there is an optimal or minimal tolerable time that groups spend in various activities. For red colobus, resting was more variable among sites than socializing, and while the combined activities of feeding and traveling were negatively correlated with resting, it was not related to time spent socializing. This suggests that when red colobus spend more time foraging, they rest less and do not adjust the amount of time spent socializing. Thus, there may be some minimum time required for socializing that is needed to maintain the social integrity of the group.

Previous investigations assessing tradeoffs between foraging and resting or socializing have produced conflicting results. ALTMANN (1980) suggested that when animals must spend greater amounts of time foraging, they would more readily allocate less time to socializing than resting. DUNBAR and DUNBAR (1988) suggested the opposite, speculating that socializing was needed to maintain social bonds. In a detailed inter-population study and a long-term intra-population study, BRONIKOWSKI and ALTMANN (1996) found evidence that increased foraging demands may result in compression of either social time or resting time, with the outcome depending on demographic characteristics of the population and the time scale used for analysis.

VALUE OF COMPARATIVE STUDIES MADE ON DIFFERENT SCALES

In this study we have documented large differences in the density and behavior of red colobus over relatively short distances (i.e. <15 km). The nature of these differences are of the magnitude often found when contrasts are made between study sites that are widely separated. Considering the data available on red colobus density clearly illustrates this point. Previous studies of red colobus outside of Kibale have estimated group density to range from 1.4 groups/km² to 2.7 groups/km² (Fig. 4). The range of densities found in Kibale surpasses that reported elsewhere (0.7 groups/km² to 7.4 groups/km²).

Comparisons made over small spatial scales offer a number of potential benefits. (1) Studies can be conducted by the same observer using the same methodology. This eliminates the possibility that differences found among populations are simply the result of differences in the methodology used by different observers. (2) At small spatial scales, phylogeny is controlled for since contrasts can be made within a species and among subpopulations for which there is genetic exchange. (3) Un-measured ecological parameters (e.g. composition of the predator community) are less likely to differ between neighboring populations than would be the case if contrasts were made among widely separated populations.

If our assessment of how ecological parameters influence behavioral patterns is influenced by

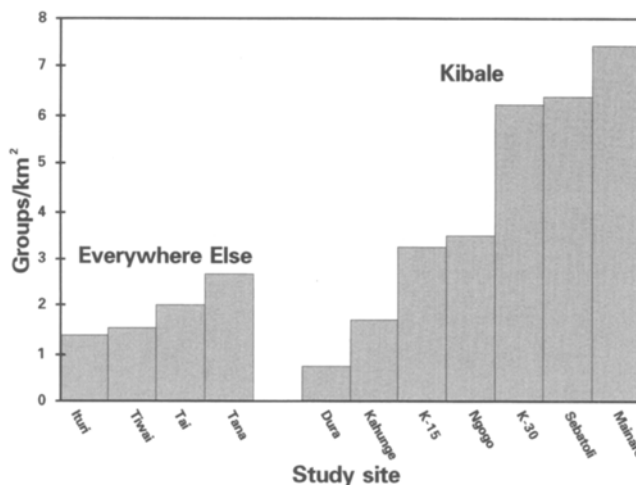


Fig. 4. The density of red colobus groups at seven sites in or near Kibale National Park, Uganda (this study) and at four other African sites. Ituri Forest, Democratic Republic of the Congo (THOMAS, 1991); Tiwai Island, Sierra Leone (OATES et al., 1990); Tai National Park, Côte d'Ivoire (GALAT & GALAT-LUONG, 1985); Tana River, Kenya (MARSH, 1986).

the scale of the study, then the value of addressing such questions at different scales should be critically evaluated. This study suggests that examining small scale variation in social behaviors, primate density, and ecological parameters will prove to be a profitable approach for understanding ecological determinants of primate behavioral patterns and abundance.

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