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Seasonal Variation in the Feeding Ecology of the Grey-Cheeked Mangabey (*Lophocebus albigena*) in Cameroon

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Seasonal fluctuations in resource abundance often cause primates to change their feeding behavior and ecology. The objective of this study was to examine the response of a largely frugivorous monkey, the grey-cheeked mangabey (*Lophocebus albigena*), to seasonal variations in fruit abundance. We used 15-min scan sampling to quantify feeding, activity, and habitat use by monkeys between February and December 1998 in the Dja Reserve, Cameroon. *L. albigena* were found to have omnivorous feeding habits, consuming the fruits, seeds, leaves, and flowers of 132 plant species. Although monkeys fed from many plant species, only five plant species accounted for 45% of all feeding records. The number of feeding observations on a plant species was significantly correlated with its fruit production. *L. albigena* responded to fruit-lean periods by shifting from a diet dominated by fruit to one dominated by seeds, flowers, and young leaves. This diet shift coincided with greater use of swamp habitat and higher dietary diversity. *L. albigena* spent the greatest percentage of scan samples feeding and traveling, but activities varied significantly over the day. Individuals spent a significantly higher percentage of scan samples feeding during the fruit-rich season than in the fruit-lean season. Comparing our results to those of studies in Gabon and Uganda, we found that *L. albigena* differ across regions in the number of plant species they consume and time spent feeding. These differences may be a result of variations in tree diversity or the strength of seasonal fluctuations in resource abundance among sites. Am. J. Primatol. 54:91–105, 2001. © 2001 Wiley-Liss, Inc.

Key words: mangabey; *Lophocebus albigena*; Cameroon; feeding ecology; seasonality; activity budget

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INTRODUCTION

Most tropical forests have distinct dry and rainy seasons that influence food production by tropical plants [Tutin & Fernandez, 1993; Janson & Chapman, 1999]. Seasonality of food production in tropical forests affects primate behavior and social organization, impacting primate populations most strongly during times of resource limitation [Terborgh, 1986]. Primates respond to variation in seasonal resource abundance by shifting diets to alternate plant products [Remis, 1997; Tutin et al., 1997], losing weight [Goldizen et al., 1988], and increasing the amount of time spent feeding [Overdorff, 1996] or traveling [Chapman, 1988]. Individuals must be flexible and capable of shifting diet and/or activity patterns as preferred foods dwindle or face lower survivorship.

Seasonal variation of fruit abundance in tropical forests depends on plant species composition, soil, and climatic conditions. Given these site-specific conditions, it is not surprising that few consistent patterns have emerged to characterize primate diets across regions. Studies have found variation in food habits both among years [Chapman, 1987] and sites [Gautier-Hion et al., 1993]. Understanding the degree to which variation in diet is due to interregional differences or seasonality first requires that seasonality of diet be understood for a particular site.

We report the feeding ecology and activity budget of one group of grey-cheeked mangabeys (*Lophocebus albigena*) in the Dja Reserve, Cameroon, to examine the effects of seasonal changes in fruit abundance on diet, behavior, and habitat use. Then we compare our findings with those of studies from the Kibale National Park, Uganda [Waser, 1977; Olupot, 1998], and the Lopé Reserve, Gabon [Ham, 1994], to determine if the feeding ecology of *L. albigena* is variable across regions. This study is important because it presents the first long-term data for *L. albigena* in Cameroon, and it takes advantage of previous research examining patterns in primate feeding ecology across Africa. The addition of data from Cameroon allows us to ask whether *L. albigena* groups in West Africa are more similar to each other or to those in East Africa.

METHODS

Study Area

This research was conducted in the Dja Reserve, south-central Cameroon. The reserve encompasses 526 km^2, making it the largest protected area in Cameroon. The mature forest study area is a 25-km^2 site centered on the Bouamir Research Station (BRS). The vegetation is semideciduous tropical rain forest [Letouzey, 1968], and has never been logged. Small-scale agriculture took place at one corner of the study site more than 90 years ago [Whitney & Smith, 1998], but the only evidence of farming is a small patch (<25 m^2) of thick *Marantaceae* shrubs devoid of large trees. The main study area contains primary forest, *Uapaca* swamp, *Raphia* swamp, and inselberg (rock outcroppings frequently covered by shallow soils and grasses) habitat. The climate is characterized by two wet and two dry seasons, with major and minor rainfall peaks in September and May, respectively [Whitney & Smith, 1998]. Average annual rainfall at the study site is approximately 1,600 mm.

Fruit Abundance

To estimate fruit abundance we used the raked-trail survey method [Zhang & Wang, 1995]. A 4.3-km-long, 0.7-m-wide trail was walked bimonthly. To avoid disturbance associated with cutting a trail, researchers selected the former hunting trail because it sampled habitats in approximate proportion to habitat abundance [Whitney & Smith, 1998]. All fruits encountered along the trail were identified to species, and the number of mature and immature fruits of each species was recorded. The trail was then cleared so that the fruits would not be counted on the next sampling date.

Phenology of fruiting trees was monitored by visual inspection of tree crowns. A total of 340 individuals of 38 species were checked at monthly intervals for flowers, leaf flush, immature fruits, and mature fruits. Trees were graded on a scale of 0 to 4 to reflect percent of full flowering or fruiting (0 = 0%; 1 = 1–25%; 2 = 26–50%; 3 = 51–75%; 4 = 76–100%). Tree species were selected in 1993 as important species in the diets of hornbills based on observations by local Baka guides and reports in the literature. Therefore, the species of trees monitored represent a subset of the total tree species in the forest and in the diet of *L. albigena*. For this reason, calculations of fruit abundance are based on the raked-trail method, whereas leaf production and flower abundance are determined by visual inspection of tree crowns. However, the subset of species monitored for phenology accurately reflects the phenology of mangabey food trees. *L. albigena* fed on some part (fruit, leaves, seeds, or flowers) of 30 (80%) of the 38 tree species monitored for phenology. Furthermore, patterns of leaf production and flower abundance of the 30 mangabey food trees examined were similar to the pattern produced by all 38 species. We report leaf production and flower abundance as the average score for all individuals each month (n = 340). Daily precipitation was recorded with a rain gauge located in a forest gap.

Feeding and Behavioral Observations

Diet and behavioral data were collected from one group of approximately 16–22 unmarked individuals of *L. albigena* that was habituated and then followed for 11 months, between February and December 1998. The group consisted of five males (two adults and three subadults), 10 adult females, and seven juveniles (four males and three females). Individuals were categorized into age/sex classes according to the characteristics given in Waser [1974]. We observed the group continuously from dawn (06:00 hr) to dusk (18:00 hr) for an average of 12 days per month in two 6-day blocks, during the first and second halves of the month. However, in December the group was followed for only 6 days.

On each of the days of observations behavioral data were collected using 5-min scan sampling periods at 15-min intervals. The methodology used in this study follows Waser [1977] and Ham [1994], and percentages of activity or feeding scan samples reflect percentages of activity or feeding times [Waser, 1975]. During each scan, the activities of as many individuals as possible were recorded. Observers recorded the time of day, location, habitat, group size, group composition (age and sex), and activity. The first activity maintained for at least 5 sec by an individual was scored. Individuals were never scored more than once during a scan. Between scans, observers searched for other nearby individuals of *L. albigena* so that all individuals in the group were included, and to avoid bias towards certain individuals or a particular age-sex class. Recorded behaviors included *feeding*, *searching* (for insects), *traveling*, *resting*, *social behavior*, and *other activity*. To ensure interobserver reliability, all observers agreed a priori on the definition of behavior categories. In addition, J.R.P. occasionally accompanied other observers as they watched the group to ensure that behavioral categories were scored consistently.

Feeding was defined as manipulating a food item and bringing it to the mouth. Both food species and food item (fruit, seed, leaf, flower, bark, pith, insect, and animal) were recorded for every feeding observation. A feeding observation is defined as the consumption of a plant species during a 15-min scan, irrespective of the number of *L. albigena* feeding. Because unusual diet items are likely to be missed between scan periods, we recorded novel diet items observed outside scan periods. Seed-eating was distinguished from fruit-eating whenever monkeys extracted seeds from the fruit and ignored the mesocarp. Monkeys rarely crushed the seed, and swallowed both the crushed seed and mesocarp. However, the few instances in which *L. albigena* swallowed both the crushed seed and fruit mesocarp were treated as seed-eating. The height at which individuals fed in the canopy was recorded categorically: (0–10, 11–20, 21–30, and >30 m).

Social behavior was defined as an interaction between two or more individuals, and included playing, chasing, grooming, copulating, and fighting. *Traveling* was recorded when the focal animal was walking, running, climbing, or leaping. *Searching* was scored whenever a monkey manipulated a substrate (i.e., broke branches or removed bark from a tree) in search of insect prey. *Resting* was defined as inactivity. *Other activity* was defined as any activity that was not associated with other categories, such as manipulating items in cheek pouches, masturbating, defecating, and self-grooming.

Between February and December of 1998, the group was observed for 1,483 hr over 132 days, for a total of 5,918 scans. Approximately half of the individuals in the group (average number = 9.57 individuals) were sampled during each observation period.

Data Analysis

Feeding, activity, and habitat use by *L. albigena* were quantified with scan sampling. One problem inherent in scan sampling is that data points are not independent. To ensure that the activities scored did not depend on those scored 15 min previously, we compared the monthly proportion of scan samples that each activity was observed using 15- and 60-min scan intervals. We chose 60-min scan samples because *L. albigena* almost never maintained an activity for 60 min [Waser, 1977; Ham, 1994]. There were no significant differences for feeding ($\chi^2 = 14.77$, df = 10, $P > 0.10$), searching for insects ($\chi^2 = 14.77$, df = 10, $P > 0.20$), traveling ($\chi^2 = 13.57$, df = 10, $P > 0.10$), social behavior ($\chi^2 = 17.59$, df = 10, $P > 0.05$), or other activity ($\chi^2 = 14.77$, df = 10, $P > 0.20$). The number of observations spent resting was significantly different between 15- and 60-min scans, ($\chi^2 = 47.50$, df = 10, $P < 0.01$), indicating that 15-min intervals were likely dependent on each other. Therefore, the percentage of scans spent resting was calculated using 60-min scan intervals. For all other activities, we found 15-min intervals to be appropriate, and pooled data for further analyses.

To examine seasonal variation in diet we used the Shannon-Weaver index of diversity. Although the Shannon-Weaver index is sensitive to sample size [Austin, 1999], it was also reported by Ham [1994] and Waser [1975], and we use it to facilitate comparisons among studies. To determine if *L. albigena* selected diet species based on their relative abundances on the study site, correlation analysis was used to compare the number of feeding observations on a given tree species and its relative importance on the study site. The relative importance of a tree species was calculated using relative density + basal area + relative frequency (M. Fogiel, unpublished data). Correlation analysis was used to test relationships between variables when appropriate. Feeding height data were compared for seasonal differences using G-tests of independence in two-way contingency tables. The daily proportions of activities and food items consumed were normalized by arcsine (square root) transformation and tested for significant differences among periods of the day and seasons using an ANOVA [Zar, 1999]. Tukey post hoc tests were conducted when appropriate. StatView 4.5 and SPSS version 9.0 were used to perform all statistical analyses.

RESULTS

Fruit, Flower, and Leaf Abundance

During 1998, a total of 18,173 fruits (mean = 1,514 fruits per month, range = 750–2,247) from 176 tree and liana species (mean = 53 species per month, range = 44–74) were counted along the raked fruit trail. Fruit abundance was highest in July, with a fourfold increase in fruit between the fruit low and fruit high. Rainfall was bimodal, with peaks preceding and following the peak in fruit abundance (Fig. 1a). Flower abundance and leaf production reached their highest levels in March and April, respectively (Fig. 1b). To more easily discuss results based on fruit abundance, we define a single fruit-rich season from May through September and two lean periods (February–April and October–December) (Fig. 1a).

Overall Diet

Although fruit and seeds made up the largest proportion of the diet (33% and 29%, respectively), *L. albigena* is omnivorous and consumed many plant parts (buds, bark, flowers, fruit, leaves, pith, and seeds), insects, and animals (Fig. 2). Diet items were distributed across 38 plant families and 132 plant species, including 11 unidentified species of plant. Monkeys frequently ate multiple parts of a single plant. For example, individuals ate both the seeds and flowers of *Pentaclethra macrophylla*.

L. albigena frequently searched for invertebrate prey, especially ants, ant larvae, and caterpillars, comprising 10% of all observations and 27% of all feeding records. Because this behavior was scored whenever monkeys searched for insects, it is likely an overestimation of the importance of insects in the diet. Individuals frequently broke hollow, dead branches, licking the ends for ants and ant larvae, but their success at finding insect prey could not be accurately measured.

On two occasions, we recorded *L. albigena* feeding on mammalian prey: an Allen's squirrel galago (*Galago alleni*) and a rope squirrel (*Funisciurus* sp.). These are the first observations of predation on mammals by *L. albigena*. In both cases, a male monkey caught or found the prey and consumed most of it while the rest of the group waited below in the canopy for dropped pieces of the prey (Poulsen and Clark, unpublished manuscript).

Seasonal Changes in Diet

Monkeys ate significantly more fruit and less leaves and flowers during the fruit-rich period than during either fruit-lean period (Fig. 2, fruit: ANOVA, F = 30.645, df = 2,132, $P < 0.001$; leaves: F = 35.798, df = 2,132, $P < 0.001$; flowers: F = 9.80, df = 2,132, $P = 0.002$; seeds: F = 0.110, df = 2,132, $P = 0.741$). Consumption of fruit peaked during the fruit-rich period, and was lowest between October and December. The monthly percentage of scan samples that consisted of fruit was significantly correlated with fruit abundance ($r_s = 0.891$, n = 11, $P < 0.01$).

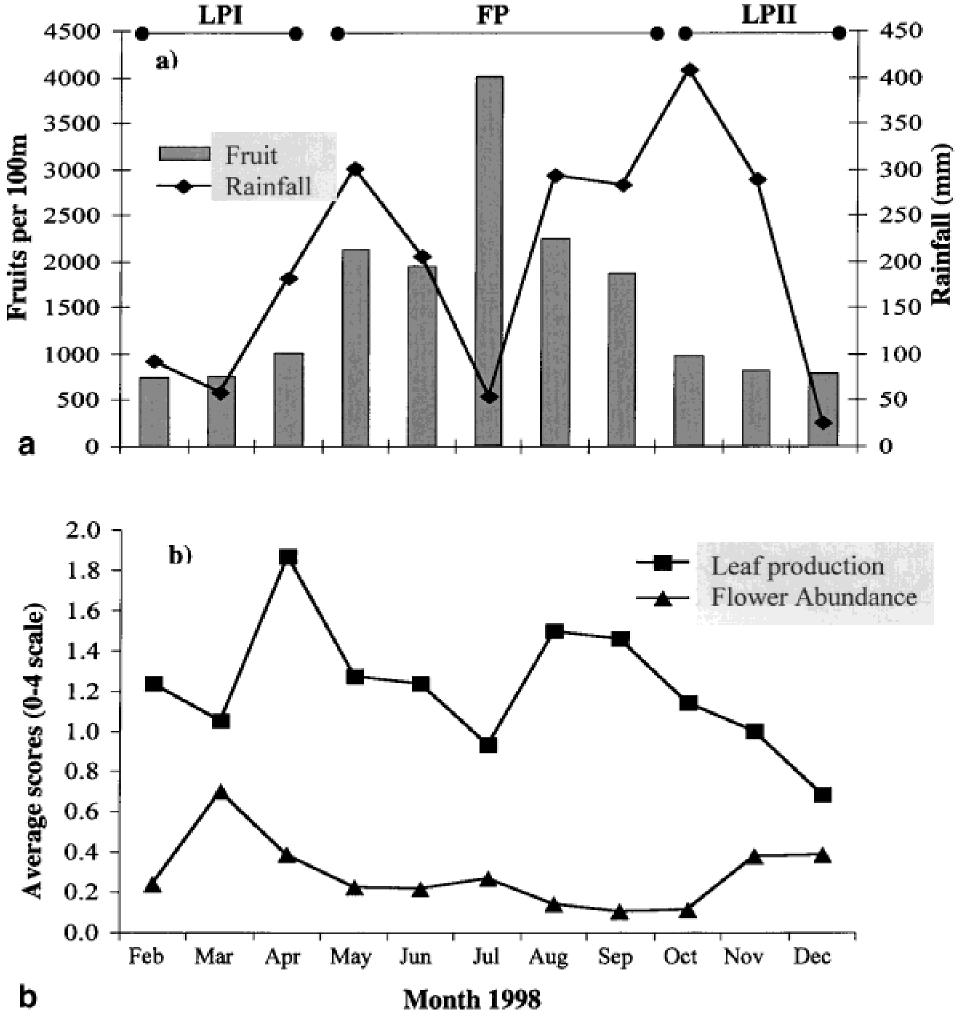

Fig. 1. **a:** Average fruit abundance per month was determined using the raked-trail survey method. Horizontal bars indicate seasons: (LP = fruit-lean season, here divided into two periods; FP = fruit-abundant period). Rainfall was collected at the Bouamir Research Station and averaged by month. **b:** Monthly leaf production and flower abundance were estimated by checking the crowns of over 300 trees monthly. Leaf production and flower abundance were scored on a 0–4 scale and averaged for a particular month.

L. albigena not only shifted to different food items between the fruit-rich and fruit-lean seasons, they also changed their resource use between lean period I and lean period II. For example, during fruit-lean period I (February–April), individuals ate leaves and flowers in a significantly higher percentage of scan samples than during fruit-lean period II (October–December) (Table I). *L. albigena* consumed seeds in a significantly higher percentage of scan samples during the second fruit-lean period than the first fruit-lean period or the fruit-rich period (Table I). Leaf production peaked between February and April, but leaf consumption was independent of leaf production (r_s = 0.105, n = 11, P = 0.759). Although leaf production reached a second high in August and September, *L. albigena* did not increase their intake of leaves during those months.

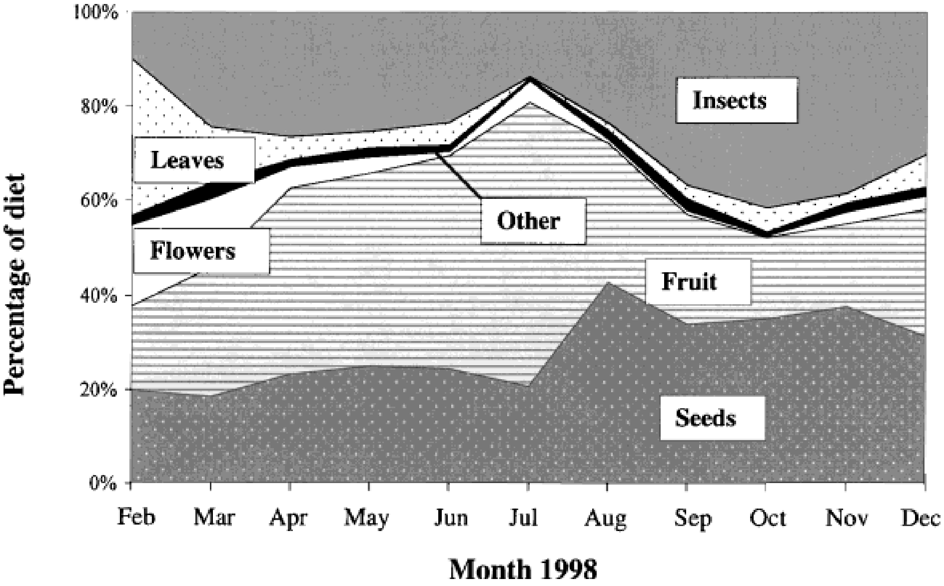

Fig. 2. The percentage of scan samples that a food item was consumed by *L. albigena* for each month. Percentages were calculated as the number of scan samples that a food item was eaten divided by the total number of scan samples for the month. The food item was only counted once per scan sample, regardless of the number of monkeys eating it.

Flowers were most abundant between February and April, and the proportion of flowers in *L. albigena's* diet was significantly correlated with flower abundance (r_s = 0.700, n = 11, P = 0.016).

Dietary Diversity and Selection

Although *L. albigena* consumed at least one part (fruit, flower, seed, bud, etc.) of 132 plant species, 25 plant species accounted for 80% of all feeding observations. Ten species accounted for over half of all feeding observations (Table II). These results suggest that *L. albigena* concentrated on a few species, but opportunistically consumed a large number of other species.

The finding that five plant species account for 45% of all feeding records

TABLE I. Proportion of Observations Spent Feeding on a Particular Plant Food Item Per Seasonal Period

Season	Fruit	Seeds	Flowers	Leaves	Pith/bark
Lean period I (February–April)	37 (485)	26 (347)	15 (199)	19 (257)	3 (39)
Fruiting period (May–September)	54 (1713)	38 (1212)	3 (94)	3 (92)	2 (69)
Lean period II (October–December)	31 (344)	58 (652)	3 (29)	7 (74)	2 (28)

The total number of scans that a food item was recorded is shown in parentheses. *L. albigena* fed on significantly greater levels of leaves (ANOVA, F = 32.315, df = 2,132, P < 0.001) and flowers (ANOVA, F = 20.614, df = 2,132, P < 0.001) during LPI than FP or LPII. *L. albigena* consumed more seeds during LPII than LPI (ANOVA, F = 46.969, df = 2,132, P < 0.001 or FP (P < 0.001).

TABLE II. List of the Ten Most Frequently Consumed Plant Species*

Species	Family	Percent feeding records
Erythrophloem suaveolens	Caesalpinioideae	17.3
Enantia chlorantha	Annonaceae	10.3
Xylopia hypolampra	Annonaceae	7.6
Polyathia suaveolens	Annonaceae	4.8
Xylopia rubescens	Annonaceae	4.8
Anthonotha sp.	Caesalpinioideae	3.7
Heisteria zimmeri	Olacaceae	3.4
Landolphia sp.	Apocynaceae	2.9
Celtis mildraedii	Ulmaceae	2.3
Pentaclethra macrophylla	Mimosoideae	2.1

*Combined, these species account for 57.5% of all feeding observations.

suggests that *L. albigena* strongly prefer these foods. This apparent preference, however, may be a product of availability of food species in the forest. The proportion of scan samples in which *L. albigena* foraged on 89 species of tree in their diet was positively correlated with the relative importance of the tree species on the study site ($r_s = 0.287$, $P = 0.006$). However, when only the 10 species most commonly recorded in scan samples were tested, there was a significant negative correlation between the number of scans spent foraging and a tree species' relative importance at BRS ($r_s = -0.673$, $P = 0.033$). Thus, *L. albigena* were probably not selecting the most important diet species based strictly on the abundance of the tree species in the environment.

A plant species may be abundant on the study site but produce little or no fruit during a given period of time. Data from the raked-trail survey indicate that *L. albigena* consumed fruits and seeds according to their availability on the study area. The number of feeding observations on a plant species was significantly correlated with its production of fruit ($r_s = 0.408$, $P < 0.001$, n = 114).

Annual dietary diversity of plant food items, calculated with Shannon-Weaver, was 3.51, and monthly dietary diversity ranged from 1.93 to 2.96. Dietary diversity was lowest during the months of September, October, and November, and was highest in April, June, and July. The diet of *L. albigena* was least diverse during the months of September through December, during which *L. albigena* specialized on the seeds of *Erythrophloem suaveolens*. Dietary diversity was not significantly correlated with monthly fruit abundance ($r_s = 0.155$, n = 11, $P = 0.65$).

Habitat Use

Seasonal differences in resource availability may cause primates to use their habitat differently. Because monkeys consumed significantly different food items during the fruit-rich period, fruit-lean period I, and fruit-lean period II, we tested for differences in foraging heights among periods. *L. albigena* foraged at significantly different heights during these periods ($G = 369.64$, df = 6, $P < 0.01$), although most feeding took place between 21–30 m in the canopy, irrespective of the season. Monkeys foraged more frequently at lower strata during lean period I compared to the other two periods, with the greatest numbers of observations at the 0–10 m and 11–20 m levels. Lower feeding heights reflect a greater use of swamp habitat (18%) during this period than on average (8%). The canopy of the swamp habitat is lower than the canopy of forest habitat (Poulsen, personal observation). During the fruit-rich period, feeding was concentrated in the mid-canopy (11–20 and 21–30 m). *L. albigena* foraged higher in the canopy during lean period II, feeding most frequently at the 21–30 and >30 m strata. This shift to slightly higher strata is likely influenced by the high frequency of observations in *Erythrophloem suaveolens*, an emergent canopy tree.

Although *L. albigena* are primarily arboreal, on occasion individuals descended to the ground to forage on fallen food items. Monkeys consumed fruits of *Annonidium mannii* and *Landolphia* spp., and seeds of *E. suaveolens* on the ground.

Daily Activities

Averaged across the year, *L. albigena* spent the greatest proportion of scan samples feeding on plants and traveling. The study group spent approximately 20% of scan samples searching for insects and resting, and they engaged in social behaviors and other activities for only 9% of all observations (Fig. 3).

We divided the day into three periods: morning (06:00–10:00 hr), midday (10:00–14:00 hr), and afternoon (14:00–18:00 hr) to test for diurnal patterns in behavior (Table III). ANOVA was performed using Type III sums of squares to test for differences in activity patterns during different periods of the day and between seasons (fruit rich and fruit lean). Significant diurnal variations among morning, midday, and afternoon were found for the following activities: searching, traveling, resting, social behavior, and other activity (Table III). Feeding by *L. albigena* did not differ among the three periods. Most varia-

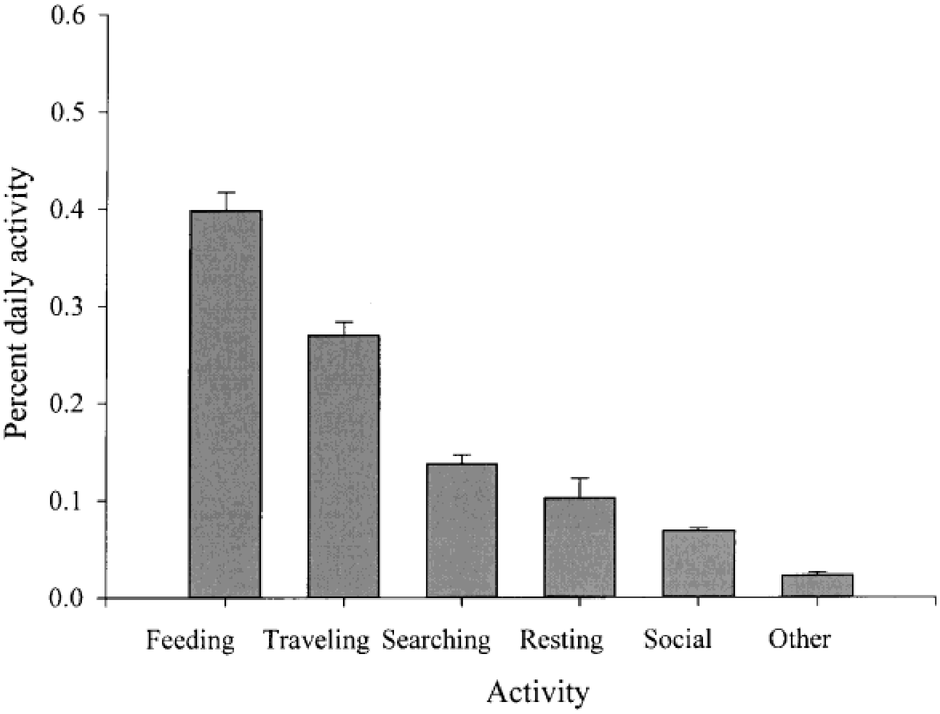

Fig. 3. Percentage of observations that *L. albigena* was engaged in each activity averaged across the year with standard error bars.

TABLE III. ANOVAs of *L. albigena* Activities (Arcsine Square Root–Transformed) Using Type III Sums of Squares

Source	SS	df	MS	*F*	*P*
A. Feeding					
P	0.022	2	0.011	0.488	0.61
S	0.658	1	0.658	29.230	< 0.001[a]
P x S	0.118	2	0.059	2.617	0.07
B. Searching					
P	0.550	2	0.275	10.121	< 0.001[a]
S	0.005	1	0.005	0.172	0.68
P x S	0.041	2	0.026	0.757	0.47
C. Traveling					
P	0.134	2	0.067	3.863	0.022[a]
S	0.003	1	0.003	0.180	0.671
P x S	0.061	2	0.031	1.767	0.172
D. Resting					
P	0.859	2	0.430	23.770	< 0.001[a]
S	0.579	1	0.579	32.049	< 0.001[a]
P x S	0.034	2	0.017	0.944	0.390
E. Social behavior					
P	0.184	2	0.092	5.913	0.003[a]
S	0.010	1	0.010	0.618	0.432
P x S	0.072	2	0.036	2.325	0.099
F. Other activity					
P	0.098	2	0.049	5.572	0.004[a]
S	0.002	1	0.002	0.215	0.643
P x S	0.117	2	0.006	6.667	0.001[a]

P and S represent period of day (morning, midday, and afternoon) and season (fruiting or non-fruiting), respectively.

[a] Statistically significant.

tion in diurnal activity is attributable to the habit of replacing feeding, traveling, and searching with resting and social behavior just before sleeping at night. Resting and social behavior occurred significantly more frequently during the afternoon period than either the morning or midday. Frequency of traveling was slightly lower in the afternoon relative to morning and midday. Searching was more frequent at midday when *L. albigena* spread out as they foraged for insects.

Seasonal Activities

Monkeys spent a significantly higher percentage of scan samples feeding during the fruit-rich period than the fruit-lean period (Table III). The percentage of observations of feeding on plant items peaked in June and August and was lowest during September through November. Feeding and resting are inversely related: *L. albigena* spent significantly fewer scan samples resting during the fruit-rich period (Table III). Significant interaction effects of season and period of day only emerged for other activity, indicating that *L. albigena* most commonly engaged in these activities during the mornings of the fruit-rich season and the afternoons of the fruit-lean season. Monthly fruit abundance was significantly negatively correlated with resting ($P < 0.001$). None of the other activities were significantly correlated with fruit abundance.

DISCUSSION

Seasonality

Fruit resources in the Dja Reserve exhibited differences in availability across the year, and *L. albigena*, like other frugivorous primates [Remis, 1997; Tutin et al., 1997], adjusted their behavior accordingly. *L. albigena* demonstrated marked seasonal variation in the types of food items consumed and percentage of scan samples spent feeding and resting as a response to differences in fruit availability.

The types of food items consumed varied seasonally, as shown by: 1) increased consumption of fruit during the fruit-rich period, and 2) decreased fruit consumption and increased feeding on seeds and leaves during fruit-lean periods. Seeds were consumed more often following the fruit abundant season when succulent fruit was scarce. However, September was an exception to this rule, as monkeys ate lower percentages of fruit and higher percentages of seeds despite a relatively high availability of fruit. During the first fruit-lean period, February through April, *L. albigena* increased their consumption of flowers and leaves relative to the rest of the year. This diet shift coincided with greater use of swamp habitat and higher dietary diversity than during the fruit-lean period between October and December. A shift in diet and habitat may allow *L. albigena* to survive fruit scarce times and reduce competition with other frugivorous monkeys and birds [Tutin et al., 1997; Poulsen et al., in press].

Primate species sympatric with *L. albigena* in the Dja also demonstrate seasonal shifts in food items eaten during fruit scarce months [Poulsen et al., in press]. Many cercopithecines shift their diets to include “fall-back” foods when preferred high-quality foods are seasonally scarce [Strier, 1999]. Gautier-Hion et al. [1993] suggested that leaf- or seed-eating might be a last resort for primarily frugivorous primates. Thus, shifting the types of food items eaten appears to be a common strategy for primates faced with fluctuations in fruit availability [Doran, 1997; Strier, 1999].

Previous studies report that primate groups travel farther and feed more when food is scarce or when food is patchy or clumped [Chapman, 1988; Overdorff, 1996]. In this study, *L. albigena* showed no seasonal differences in the proportion of scans spent traveling. Feeding increased during the fruit-rich season, rather than when food was scarce. Increased feeding during the fruit-rich period may be a result of decreased resource patchiness compared to fruit-lean periods. Between September and December, *L. albigena* largely specialized on the seeds of *Erythrophloem suaveolens*, a large-canopied, emergent tree that produced large numbers of fruits allowing for high foraging efficiency. Easy access to the seeds of *E. suaveolens* in September may also have contributed to their increased consumption of seeds in this month, even though fruit availability was relatively high. Alternatively, monkeys may feed more during fruit-rich times solely because fruit is more abundant or because they need to consume more fruits to attain a minimum caloric or nutrient intake.

The diet of *L. albigena* is likely constrained by resource availability. We found that the ten most important species in the monkey’s diet were not among the most important tree species on the study site. These tree species were the most productive species in 1998; and consumption of fruit and seed species was significantly correlated with fruit abundance. It appears that when *L. albigena* can be selective, they choose fruit and seeds over leaves. Despite a peak in leaf production in August and September, monkeys did not alter their consumption of fruit and seeds to eat more leaves. The high number of plant species in the diet of *L. albigena* may partially be explained by the fact that 1998 was a fruit-lean year in the Dja Reserve compared to the previous three years of study (Poulsen, unpublished data). The climatic and rainfall conditions that lead to seasonal fluctuations in primate resources may also lead to substantial year-to-year variation [Tutin & Fernandez, 1993]. Therefore, *L. albigena*'s broad diet may be a result of trying to gain adequate food during a fruit-scarce year.

Comparison With Other Studies

Few studies have compared the ecology of conspecific primates at different sites across Africa. However, such comparisons are important because they can 1) determine the ability of primates to change food habits with changing resource availability, and 2) test which environmental factors most strongly affect primates. Furthermore, geographical differences in primate ecology and behavior may emerge from comparative studies, such as Gautier-Hion's [1983] hypothesis that primates in West Africa consume more succulent fruit than those in East Africa. The comparison of our study of *L. albigena* feeding ecology to previous studies is limited by the number of microhabitats that are compared, since only three studies at two different locations (Lopé Reserve, Gabon, and Kibale National Park, Uganda) employed similar methods over a similar amount of time. Furthermore, by comparing groups of *L. albigena* at different protected areas in Africa, we implicitly assume that ecological variables important to the feeding ecology of mangabeys will likely vary more between distant sites (across Africa) than among neighboring sites. With these caveats in mind, we compare results of our study with those of similar studies at the Lopé Reserve, Gabon [Ham, 1994], and the Kibale National Park, Uganda [Waser, 1977; Olupot, 1998]. Ideally, cross-continent studies should be conducted concurrently with previously agreed upon methodologies. To date, no such study has been done, probably because of the logistical difficulties involved. However, broad comparisons between sites are appropriate because all three studies were conducted for similar periods of time using the same general methodology. Our cross-continent comparisons suggest the following trends: 1) The feeding ecology of *L. albigena*, most notably the number of plant species consumed and the percentage of scan samples spent feeding, varies across African sites. 2) *L. albigena* groups in West Africa are similar in that they eat a higher number of plant species, spend more time feeding, and consume high percentages of seeds (Table IV).

When seeds are considered a subset of fruit, *L. albigena* consume similar proportions of food items across regions of Africa, making them appear highly frugivorous (Table IV). However, when seeds are distinguished from fruit, *L. albigena* is better characterized as a frugivore-granivore. In Kibale, the proportion of seeds in the diet of monkeys was not quantified, but their diets may also consist of relatively high quantities of seed (Olupot, personal communication). Waser [1977] reported that granivory by *L. albigena* involves a fairly large number of species, but that the species are not common in the diet. To date, evidence does not support Gautier-Hion's [1983] statement that primates in West Africa consume more succulent fruit than those in East Africa, but seed-eating in East Africa should be better quantified.

Greater tree diversity may be one factor contributing to the more diverse diets of monkeys at Kibale compared to those in the Dja and Lopé. Even though the number of plant species consumed by *L. albigena* in the Dja was greater

TABLE IV. Proportion of Diet Composed of Each Food Item, Number of Diet Species, and Proportion of Total Scans Spent Feeding on Food by *L. albigena* Groups Across Central Africa

		Food items					Diet	% scans
Study	Location	FR / SD	LV	FL	IN	OT	Spp	feeding
Present study	Dja Reserve, Cameroon	62 / (29)	5	4	27	2	132	50
Ham [1994]	Lopé Reserve, Gabon	66 / (35)	4	2	28	0	75	66
Olupot [1998]	Kibale National Park, Uganda	59 / (–)	5	5	27	4	51	–
Wallis [1979]	Kibale National Park, Uganda	61 / (8)	13	0	12	1	51	–
Freeland [1980]	Kibale National Park, Uganda	58 / (–)	10	0	25	2	29	–
Waser [1974]	Kibale National Park, Uganda	59 / (–)	4.3	3.4	31	2.5	62	43

In this table, fruit consists of any part of the fruit including seeds. (Seeds) reports the proportion of observations on fruit in which the seeds were fed upon.
FR, fruit; SD, seeds; LV, leaves; FL, flowers; IN, insects; OT, other.

than in Lopé or in Kibale (Table IV), overall Shannon-Weaver dietary diversity was higher at Kibale (4.37) [Waser, 1975] than at the Dja (3.51) or Lopé (3.46) [Ham, 1994]. This indicates that monkeys at the Dja, and to a lesser extent at Lopé, foraged on a broad number of plant species, most of which accounted for a small proportion of their overall diets. Greater dietary diversity at Kibale may be explained by greater resource availability. Primates in a forest with higher tree-species richness will likely have more foraging options and be less likely to experience periods of food scarcity than primates at a more depauperate forest [Chapman et al., 1999a]. In fact, tree species diversity is higher at Kibale (H = 4.37) than Lopé (H = 3.35) or the Dja (H = 4.03) [Waser, 1977; White, 1992].

Alternatively, differences in dietary diversity may also be explained by seasonal variations in fruit abundance. Both the Lopé and Dja reserves demonstrate marked changes in seasons [Tutin et al., 1997], and fruiting at Kibale exhibits regular annual peaks [Chapman et al., 1999b]. Milder seasons and greater year-long resource availability may allow monkeys to be more selective in the foods they consume. Waser [1975] suggested that the effects of seasonal variation on *L. albigena* are slight at Kibale [Waser, 1975]. If, as noted above, *L. albigena* at the Dja and Lopé reserves consume more seeds than reported for Kibale, seasonal variation in fruit abundance may be a contributing factor. In habitats with more stable climatic conditions and more constant sources of fruit, primates maintain more frugivorous diets throughout the year [Moraes et al., 1998]. However, the effects of seasonal variation on dietary diversity need to be tested explicitly to determine if this contributes to the differences in dietary diversity among the three sites.

Differences in the feeding ecology of *L. albigena* groups across Africa may be due to differences in tree diversity or seasonality among sites. But intersite comparisons should be interpreted cautiously because interannual shifts in feeding ecology at a site or between two sites within the same forest may also be severe [Chapman, 1987]. If general patterns of primate ecology and behavior are to emerge, we must undertake comparative studies conducted concurrently at different locations over several years.

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