Effect of Group Size on Activity Budgets of *Colobus vellerosus* in Ghana

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Group size influences foraging efficiency in several primates. We examined the activity budgets of 3 groups of ursine colobus (Colobus vellerosus) at the Boabeng-Fiema Monkey Sanctuary (BFMS) in Ghana to determine whether larger group size induces scramble competition. We studied 2 groups (B1; N = 7 − 8 and WW; N = 31 − 33) occupying slightly overlapping home ranges from August to November 2000. We observed the third group, B2 (N = 15 − 16), comprising B1 and 7 male invaders in the same home range as B1 from August to November 2001. By comparing groups belonging to the same population and occupying sligthly overlapping or similar home ranges, we were able to control, to a certain extent, for differences in food distribution. We recorded a total of 3353 scans, yielding 14,886 activity records, over 73 days. As with other black-and-white colobus, resting was their most common activity (59%). Intergroup comparisons suggest that time spent feeding, resting and moving did not vary in relation to group size. However, intragroup comparisons between the sexes show that females in the large group spent more time feeding than males did, whereas this was not the case in the small group, which suggests that scramble competition may be occurring among female Colobus vellerosus at BFMS. It is also possible that this may be due to greater nutritional requirements because of a higher proportion of infants in the large group. In fact, the proportion is quite similar between the two groups, lending support to the idea that females in the two groups had comparable nutritional demands due to lactation. This suggests that increased feeding in females in the large group was partly an effect of scramble competition. Group size and

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group composition also influenced the frequency of social behavior. There was more grooming in the large group, and it was performed mostly by females. The distribution of activities throughout the day was similar to the pattern reported for other black-and-white colobus.

INTRODUCTION

Predation risk is theorized to set the lower limit of group size in diurnal primates, while the upper limit is set by the reduced foraging efficiency experienced by individuals in larger groups (Alexander, 1974; Terborgh and Janson, 1986; van Schaik, 1983; Williamson and Dunbar, 1999) or by social factors such as risk of infanticide (Steenbeek and van Schaik, 2001). Scramble competition—the effect of group size on foraging efficiency—can be detected in several ways. The two most frequently used methods to infer scramble competition at the group level involve showing a positive association between group size and (a) day range length or (b) time spent moving and feeding (Chapman and Chapman, 2000; de Ruiter, 1986; Dunbar, 1992; Isbell, 1991; Isbell and Young, 1993; Steenbeek and van Schaik, 2001; van Schaik *et al.*, 1983).

Factors other than group size can also influence activity budgets. For instance, different nutritional requirements between males and females, can affect feeding time (Schoener, 1971). Increased feeding for females versus males occurs in some colobines and other folivore-frugivores (red colobus: Marsh, 1981; Thomas's langurs: Steenbeek and van Schaik, 2001; black howlers: Bicca-Marques and Calegaro-Marques, 1994). The spatial and temporal availability of food is another factor influencing activity budgets (Isbell and Young, 1993; Iwamoto and Dunbar, 1983; Marsh, 1981; Menon and Poirier, 1996; Oates, 1977; Watts, 1988). For instance, if a large group can maintain a better quality home-range than a small group, this could lead to a decrease in feeding and moving time, thus offsetting the negative effects of food competition in the larger group (Altmann and Muruthi, 1988; Iwamoto and Dunbar, 1983; Watts, 1988). In the absence of ecological measurements quantifying the availability and quality of food, one can compare groups that have adjacent, relatively similar home ranges, or a group for which composition changes over time while home range remains the same (Steenbeek and van Schaik, 2001).

Black-and-white colobus species vary substantially in the time they spend feeding, traveling and resting (Bocian, 1997; Dasilva, 1994; Fashing, 2001a; McKey and Waterman, 1982; Oates, 1977), but there is little

information at this time that would allow us to understand if this variation is due mainly to differences in group sizes, habitats, or diets. Indeed, few studies have data from more than one group of the same species at the same study site, which allows us to measure the effect of group size on activity budget while controlling for habitat and diet (contra Fashing, 2001a). We investigated the effect of group size on the activity budget of 3 groups of *Colobus vellerosus* in the Boabeng-Fiema Monkey Sanctuary (BFMS) Ghana, to infer whether they are experiencing intragroup scramble competition.

METHODS

Study Site

We collected data on ursine colobus (aka Geoffroy's pied or white-thighed colobus; *Colobus vellerosus*) at BFMS in the forest-savanna transition zone in central Ghana (7° 43' N and 1° 42'W). The dry semideciduous forest is a sacred grove of 192 ha (1996 UNDP Map Sheet # 0702A4), 350 m above sea level in the Nkoranza District of the Brong-Ahafo Region. The terrain is flat, with a shallow slope leading to a groundwater spring.

The vegetation is a mosaic of primary forest, regenerating farm land (secondary forest), woodland and disturbed forest along the edges. The sanctuary contains evidence of long-term human influence. Exotic trees, e.g. teaks, mangos, cocoa, are present, and local people use the forest for firewood and medicinal plant collection and to graze sheep (Saj *et al.*, in review). Our ecological survey shows that along the forest edges near the village, 22% of the trees are *Grewia mollis*, which is characteristic of disturbed forests (Hawthorne, 1990), whereas it is absent elsewhere. Our ecological survey also shows that regenerating farm lands contain a high proportion of large trees ($\geq$40 cm DBH = 46%), whereas the disturbed forest and the primary forest areas contain a smaller proportion of large trees (23–24%). The overall number of trees is smaller in regenerating farm lands, (T. Saj, unpublished data). Several economically important tree species have been protected. For instance, large mahoganies (*Khaya spp.*) are present and are an important food resource for *Colobus vellerosus*.

A census of the population of *Colobus vellerosus* at BFMS in 2000 reported 189-211 individuals in 14 groups. Group sizes vary considerably within the relatively small area of BFMS (range: 4-33, mean: 14.3, N = 14; Saj *et al.*, in review), where *Colobus vellerosus* are sympatric with a larger population of mona monkeys (*Cercopithecus campbelli*) (Kankam, 1997).

There is a marked dry season from November to February/March. The mean annual rainfall from 1985 to 1990 is 1250 ml (SD: $\pm$ 21.1; taken in

Nkoranza, 20 km from BFMS) (Fargey, 1991). During our study, we collected rainfall daily with a rain gauge in a clearing at the Boabeng-Fiema Guesthouse, <1 km away from the ranges of both study groups. During the 2000 4-mo study, 510 ml of rain fell, and during the same 4-mo period in 2001, the total rainfall was 350 ml. The 5-year mean for this period from 1985 to 1990 is 510 ml (SD: ± 25.5).

Study Groups

We studied 2 groups of Geoffroy's pied colobus from August to November of 2000 (WW and B1; Table I). They had home-ranges that overlapped by three 50×50 m quadrats, representing 8% of WW's range and 13.6% of B1's range. In April of 2001, B1 was invaded by an all-male group of 7–9 males, one of which was a juvenile. The all-male group remained in close proximity to B1, and by July 2001, 7 males—6 adults and 1 juvenile— had essentially integrated into the group: B2 (T. Saj, personal observation). An adult female transferred into B2 in October and stayed for ≥2 mo (Saj and Sicotte, 2002). We collected data on B2 from August to November of 2001 (Table I). B2 used the same home range as B1 (Saj *et al.*, 2002). Despite the fact that all 3 groups used a combination of primary, disturbed, and secondary forest, B1/B2's home range included more disturbed and secondary forest (T. Saj, unpubl. data).

Diet of the Study Groups

Colobus vellerosus at BFMS are primarily folivorous. The annual diet is made up of mature and young leaves (34% and 40% respectively), seeds and seedpods (8%), unripe fruits (8%), flowers and buds (6%). The main food tree species are in the Moraceae, Leguminosae, and Bombacaceae (27%, 23% and 19% of the diet, respectively). Seeds and unripe fruits form an important part of the diet when they are available: *Albizia coriaria, Aubrevillea kerstingii, Trilepisium madagascariense*. Monthly seed-eating ranged

Table I. Group composition and study periods

Name	Study period	Group size	Adults/subadults		Juveniles[a]		Infants[a]
			M	F	M	F	
WW	08/00–11/00	31–33	5	11	4	3–4	7–9
B1	08/00–11/00	7–8	1	3	2	0	1–2
B2	08/01–11/01	15–16	7	3–4	3	0	2

[a]We have no fully accurate count of the immatures in WW.

from 0 to 24%; monthly unripe fruit eating ranged from 0 to 23%; (T. Saj, unpubl. data).

Data Collection

Teichroeb, Saj, and 3 research assistants collected data via the frequency method (Davies *et al.*, 1999; Struhsaker, 1975). Interobserver reliability tests between all researchers gave accuracy rates of ≥96%. The protocol involved 3-day observation periods, from dawn to dusk (600 – 1800), twice a month for each group. To assure independence, the 3-day observation blocks for each group are separated by ≥7 days, except during the last month of data collection for B2 in 2001, when only 3 days were left between the last 2 observation blocks. We considered the 3-day blocks as independent units for statistical analyses. Twice when WW was lost on a full-day follow, we made up the remainder of data collection hours at the end of the 3-day follow. We took scans every 15-min throughout the full-day follows (Fashing 2001a). We avoided rescanning the same individuals from scan to scan when possible. We allotted 5 min to record the activities of ≤5 monkeys, excluding white infants 2 mo old. We left 5 sec between first spotting an individual and recording its behavior to avoid over-representing in the activity budget eye-catching behaviors such as moving. We recorded behaviors in 4 categories: feed, (manipulation and ingestion of food, noting plant parts and species), rest, move, and social. Social includes grooming, play, and copulation (state behaviors). We probably did not measure agonistic behavior and infant-transfers (event behaviors) accurately. So we exclude them from the analysis.

Data Analyses

We compared the groups in pairs (B1 vs. WW and B1 vs. B2). The comparison between B1 and WW tests for an effect of group size in the same study period between groups that have slightly overlapping home ranges. The comparison between B1 and B2 tests for changes in activity budget in a group that occupied the same home range, but increased markedly in size in the second year. A comparison between B2 and WW would not allow a test of the effect of group size, as both are large. We have no reliable datum on age-sex class categories on B2, but we collected them on the two other groups.

We transformed ratios of the number of records for each behavioral category over the total number of records into a percentage and represented the overall activity budget. Raw frequencies could not be used for statistical

comparisons because it was necessary to control for differences in group size and sex ratio between the groups. For the group comparisons, we employed ratios of the number of records for an activity in each group, over the total number of records for it. For the age-sex class comparisons, the ratios are the number of records for each age-sex class category involved in each activity over the records for the age-sex class in all activities. We compared them via Mann-Whitney U tests. The 3-day observation block is the unit of analysis (N = 8 for each group). We also broke down the social category into grooming, copulations, and play, and compared them between groups.

Since *Colobus vellerosus* is a little-known species, we also give baseline information on the distribution of activities throughout the day (N = 24). We compared daily activity patterns to see if group size affected the distribution of activities throughout the day. We compared the hourly proportion of records spent resting, feeding, moving, and being social between B1 and B2 and between B1 and WW via a Kolmogorov-Smirnov test.

All statistical tests a two-tailed and results a significant at p ≤ 0.05. We analyzed data via Statview 4.01.

RESULTS

Overall Activity Budget

We recorded a total of 3353 scans over 73 days. There is an equal number of scans for each of the 3 groups. The yielded a total of 14,886 records (5,562 for WW, 3,710 for B1, and 5,614 for B2). The average numbers of records for 100 randomly chosen scans are: B1: 3.6; B2: 4.9; WW: 4.9. The scans on B1 yielded fewer records because they had fewer individuals and were slightly less habituated than WW and B2 at the beginning of the study. The mean activity budget for the 3 groups over the study periods shows resting in 59.1% of records, feeding in 23.7%, moving in 14.6%, and social behavior in 2.6%.

Intergroup Comparisons

We first compared the records for each activity between the groups (Table II). There is no difference between B1 and B2 in any of the general activity categories (Mann-Whitney U test, $n_1 = 8$ $n_2 = 8$, feeding: $z = -0.53$, $p = 0.6$; resting: $z = -0.84$, $p = 0.4$; moving: $z = -1.59$, $p = 0.11$; social: $z = -0.81$, $p = 0.42$), though there were more copulations in B2 ($z = -3.46$, $p = 0.0005$). Copulations accounted for 36.1% of social records in B2, but only 3.2% in B1 (Fig. 1).

Table II. Statistical comparisons performed between the groups and the age–sex classes [$p \leq 0.05$]

| Comparison	Difference	Direction
Intergroup comparisons		
B1 vs. B2		
Feed	0.60	
Rest	0.40	
Move	0.11	
Social	0.42	
Grooming	0.24	
Play	0.43	
Copulations	0.0005	B2 > copulations B1
B1 vs. WW		
Feed	0.68	
Rest	0.91	
Move	0.11	
Social	0.04	WW > social B1
Grooming	0.001	WW > grooming B1
Play	0.16	
Copulations	0.37	
Ad.♂ Feed	0.71	
Ad.♀ Feed	0.56	
Ad.♂ Rest	0.75	
Ad.♀ Rest	0.27	
Ad.♂ Move	0.40	
Ad.♀ Move	0.28	
Ad.♂ Social	0.23	
Ad.♂ Grooming	0.52	
Ad.♀ Social	0.0007	WW females > social B1 females
Ad.♀ Grooming	0.0007	WW females > groom B1 females
Intragroup age–sex class comparisons		
Feed: Ad.♂ vs. Ad.♀		
B1	0.11	
WW	0.04	Females feed > males in WW
Rest: Ad.♂ vs. Ad.♀		
B1	0.27	
WW	0.08	Trend − Males rest > females in WW
Move: Ad.♂ vs. Ad.♀		
B1	0.14	
WW	0.71	
Social: Ad.♂ vs. Ad.♀		
B1	0.91	
WW	0.002	Females > social males in WW
Grooming: Ad.♂ vs. Ad.♀		
B1	0.82	
WW	0.002	Females > grooming males in WW
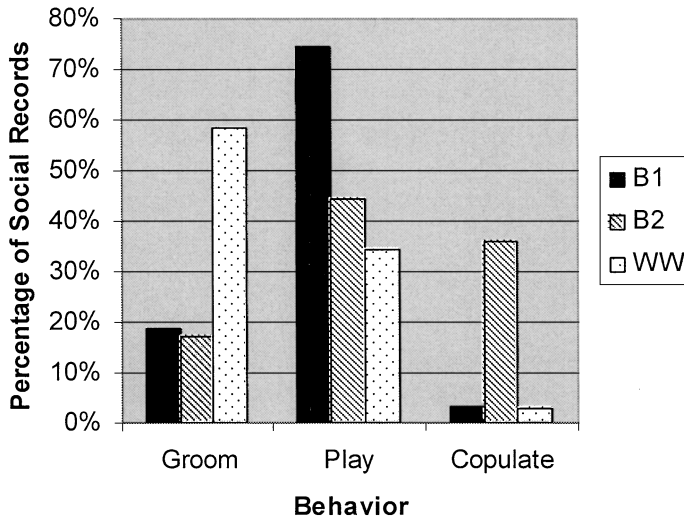
Fig. 1. Proportion of time spent grooming, playing, and copulating in the focal groups. The proportion of time is expressed as the percentage of social activity records spent grooming, playing, and copulating in B1, B2, and WW.

Comparisons between B1 and WW show no difference in the proportion of feeding ($n_1 = 8$, $n_2 = 8$, $z = -0.41$, $p = 0.68$), resting ($z = -0.12$, $p = 0.91$) or moving ($z = -1.62$, $p = 0.11$). However, social behavior was more frequent in WW than in B1 ($z = -2.08$, $p = 0.04$) and WW groomed more than B1 did ($z = -3.26$, $p = 0.001$). Grooming made up 58.5% of social records in WW and 19% in B1 (Fig. 1).

We also compared males and females separately between WW and B1. The adult males in WW and the single adult male of B1 exhibited no difference in any category ($n_1 = 8$, $n_2 = 8$, feeding: $z = -0.37$, $p = 0.71$; resting: $z = -0.32$, $p = 0.75$; moving: $z = -0.85$, $p = 0.4$; social: $z = -1.21$, $p = 0.23$). Adult females in WW and B1 exhibited no difference for feeding, resting, or moving ($z = -0.58$, $p = 0.56$; $z = -1.12$, $p = 0.27$; $z = -1.08$, $p = 0.28$, respectively). However, females in WW were more social than those in B1 ($z = -3.39$, $p = 0.0007$) and groomed more frequently ($z = -3.40$, $p = 0.0007$).

Intergroup Comparisons Between Males and Females

Females fed more than males in the large group (Mann-Whitney U: $n_1 = 8$, $n_2 = 8$, WW, $z = -2.01$, $p = 0.04$) but not more than those in the small group (B1, $z = -1.58$, $p = 0.11$). Males tended to rest more than

females in the large group (WW, $z = -1.74$, $p = 0.08$), but not more than those in the small group (B1, $z = -1.12$, $p = 0.27$). Males and females moved at the same frequency in both groups (WW, $z = -0.37$, $p = 0.71$; B1, $z = -1.48$, $p = 0.14$). Males and females were equally social in B1 ($z = -0.12$, $p = 0.91$), but females in WW were more social than males ($z = -3.16$, $p = 0.002$). Specifically, WW females groomed more than males did ($z = -3.08$, $p = 0.002$) and it was predominantly female-female and female-immature. In B1, much of the grooming was directed by the adult females towards the adult male, so neither social records nor interaction in grooming bouts differ between the sexes.

Temporal Variation in Activity Patterns

We noted no difference between the groups in the distribution of feeding, resting, moving, or social records throughout the 12-h observation days (Kolmogorov-Smirnov, $df = 11$, 8 comparisons, $p \geq 0.05$ in each case). Therefore, we lumped the data for the 3 groups to show the general distribution of daily activities (Fig. 2). Feeding records indicate a slight increase in early morning (07:00–08:00 h), at midday, and towards the end of the afternoon (16:00–17:00 h). Resting occurs at high levels throughout the day. There was an increase in movement at the end of the day (17:00–18:00 h). Social behavior occurred at a fairly constant, albeit low, level throughout the day, tapering off in the hour before dusk.

DISCUSSION

Is There an Effect of Group Size on Activity Budget?

Group size did not influence the activity budget of *Colobus vellerosus* at BFMS. Furthermore, females in the large group did not feed more than females in the small group did, which, suggests that increased group size does not result in increased intragroup scramble competition. However, intragroup comparisons of males and females show that females had more feeding records than males in the large group (WW), but not in the small group (B1).

This last result suggests that females in the large group must spend more time feeding than males do to fulfill their dietary requirements, whereas they do not need to do so in the small group. This could be due to lower encounter rates with food due to faster depletion in the large group (Chapman and Chapman, 2000). The data we present here do not allow us to test this
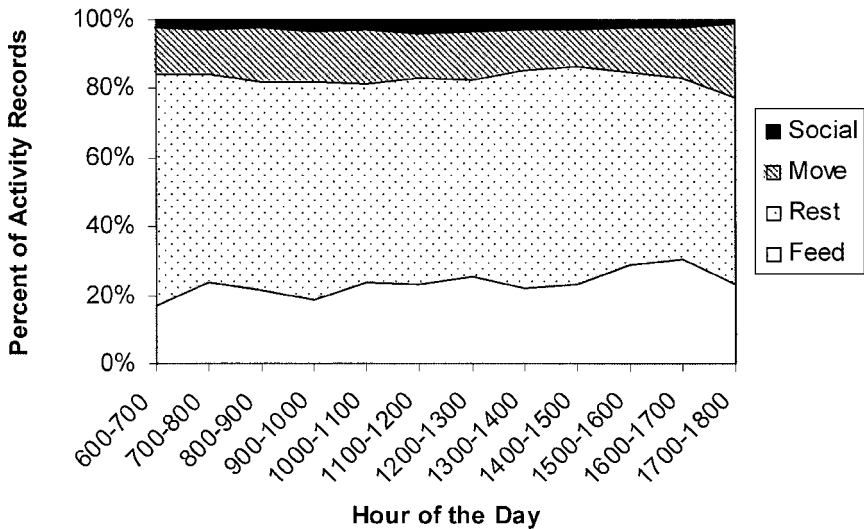
Fig. 2. Activity patterns throughout the day. Activity records for B1, B2, and WW are combined.

hypothesis. Alternatively, females in WW may have increased nutritional requirements due to a larger number of suckling infants in relation to B1. To investigate this hypothesis, one would ideally compare feeding records in females with infants and females without infants in the 2 groups. But this is not easily accomplished in *Colobus vellerosus* where in individual recognition is difficult and infant transfer is a regular occurrence. Therefore we compared the female-to-infant ratio between WW and B1 to assess whether nutritional requirements due to lactation were similar or not for the females of the two groups. In B1, the female to infant ratio was 0.66 (Table I). In WW, we calculated the ratio via the mean number of infants in the group during the study, giving a value of 0.73. The values are rather similar, suggesting that the females in the 2 groups may have comparable nutritional demands due to lactation. This suggests that increased feeding in females in the large group is probably partly explained by greater food depletion. Nevertheless, more work is required to measure encounter rates with food and food intake in female *Colobus vellerosus* in relation to group size and presence/absence of infants.

Effect of Group Size and Composition on Social Behavior

Group size and group composition had a strong effect on social behavior. Individuals in B2 engaged in more copulations than individuals in B1

did. This pattern is likely due to the unusual composition of B2. The all-male group invaded B1 in April of 2001, which resulted in a group with 7 adult males and 3 adult females. After injuring the resident male of B1, the new males began to copulate with the females, and copulations remained frequent even after the resident male recovered from his wounds and the new males formed a stable group with the members of B1 (Saj and Sicotte, 2002). Individuals in WW groomed more than those in B1. The frequent grooming in WW is probably partly explained not only by their larger group size but also by their larger number of females versus B1. This result is consistent with most studies of Old World monkeys and apes, wherein the amount of time spent in social activities increased with group size and the availability of potential partners (Dunbar, 1992).

Variation in Activity Budgets in Black-and-white Colobus

With resting records at 59% and feeding at 24% of the activity budget, BFMS *Colobus vellerosus* are similar to other black-and-white colobus in that they spent more time resting than feeding. Nevertheless, activity budgets for the 5 species of black-and-white colobus vary considerably (Table III).

The variation in activity budgets is not surprising given the range of variation in group sizes and compositions, habitats and diets of the 5 species. Black-and-white colobus form relatively small groups (range: 2–23, mean: 10.1, N = 95; Fashing, 2001a; Oates, 1994), but have a flexible social structure

Table III. Comparison of the activity budgets of black-and-white colobus groups

Species and site	Source	Group size	Feed	Rest	Move	Social
Colobus polykomos						
Tiwai	Dasilva (1992)	9–11	31	55	12	2[a]
C. guereza						
Kibale	Oates (1977)	9	20	57	5	11
Ituri	Bocian (1997)	8–10	26	44	24	5
Kakamega	Fashing (2001a)	10–13	28	63	2	6
		5–8	23	64	3	10
C. satanas						
Douala-Edea	McKey and Waterman (1982)	13–17	23	54	4	13
C. angolensis						
Ituri	Bocian (1997)	19–20	19	52	22	5
C. vellerosus						
Boabeng-Fiema	This study	31–33	24	60	12	4
		15–16	23	58	17	2
		7–8	24	59	15	2

Note. Values are percentage of time or records spent in given activity. Some of the social percentages were calculated by adding several of the original authors' categories together.
[a] Includes other, miscellaneous behavior.

with one-male and multimale groups occuring in every species (Oates, 1994). Large aggregations, where in several multimale groups coalesce, occur in *Colobus angolensis* (Bocian, 1997; Moreno-Black and Bent, 1982; Struhsaker and Leland, 1987), and appear to be permanent at one site (Fimbel *et al.*, 2001). Male-biased dispersal is apparently the norm, but data from several populations suggest that male and female dispersal can occur (*Colobus guereza*: Fashing, 2001b; *C. polykomos*: Korstjens *et al.*, 2002; *C. satanas*: Oates, 1994; *C. vellerosus*: Saj and Sicotte, 2002). Black-and-white colobus inhabit a wide range of habitats, from montane and dry gallery forests to lowland moist forests (Oates, 1994) and swamp forests (Saj and Sicotte, in review). Their diets can be diverse (≤120 plant species: *Colobus vellerosus* at Bia in Ghana; Olson and Curtin, 1984), or they can survive on monotonous diets offering little variation (*C. guereza* in fragments around Kibale; Onderdonk and Chapman, 2000). Any or all of the above factors may account for the variation in activity budgets reported for various populations of black-and-white colobus.

Differences in activity budgets may result from varying study durations and hence possibly from seasonality. Some studies of black-and-white colobus have spanned ≥1 year (Bocian, 1997; Dasilva, 1992; Fashing, 2001a; McKey and Waterman, 1982; Oates, 1977), while ours comprised 2 4-mo periods in consecutive years Nevertheless, they represent periods of wet and dry season. It is also possible that differences in data collection methods are responsible for some of the differences among studies, as the behavior recorded is sometimes the first that lasts over 3 or 5 sec (Fashing, 2001a; Struhsaker, 1975), whereas others have recorded the behavior performed 5 sec after spotting the subject (Davies *et al.*, 1999; this study). A comparison of the 2 methods of data collection and the extent to which they produce different results would help to interpret and further to compare published studies. To our knowledge, such a comparison involving the same population has yet to be done.

Distribution of Activities Throughout The Day

Our results indicate no difference between groups of *Colobus vellerosus* in daily activity pattern. There are high levels of resting in *Colobus vellerosus* with two peaks of feeding in the early morning and early evening. A less pronounced increase in feeding also occurred around midday. The patterns documented here are consistent with the daily activity patterns for feeding and resting in several other populations of black-and-white colobus (Bocian, 1997; Dunbar and Dunbar, 1974; Fargey, 1991; Oates, 1977; Rose, 1978).

CONCLUSIONS

Long-term studies that compare data from several groups in the same population are needed to better understand the effect of group size on feeding and ranging behavior in colobus and other folivore-frugivores. We also need studies that document the extent of dietary overlap, in terms of plant part and species, between males and females to get a more accurate picture of the behavioral adjustments individuals make to meet their energetic demands (Hemingway, 1999).

Nevertheless, recording activity budget remains a relatively crude way of inferring feeding competition and may not always be able to detect it. For instance, some primates increase their rate of feeding and traveling without increasing the time spent in these activities (Dunbar, 1992; Stacey, 1986). Data on individual food intake and rate of travel (Isbell *et al.*, 1998; Janson and van Schaik, 1988) would allow us to gain a more refined understanding of the extent of behavioral adjustments to a competitive situation. However, data on activity budget is probably useful for folivore-frugivores; Kurland and Gaulin (1979) reported a positive association between time spent feeding and weight of leaves consumed.

Finally, an increase in feeding (whether it is feeding time, food intake, or food quality) may not be the only strategy used to compensate for increased competition. Energy conservation by sunbathing, or hunching in cool weather while resting is possibly another way to cope with energetic demands (Oates, 1977). Seasonal changes in postures are reported for *Colobus polykomos*, which suggests that behavioral thermoregulation increases in times of low food availability (Dasilva, 1992, 1993). Whether this happens more often in females, or in large groups remains to be seen. However, it is interesting to note that huddling, another behavior that can have a thermoregulatory function (Schino and Troisi, 1990), does not seem to occur in *Colobus vellerosus*. Whether this is due to weak female-female relationships or to an actual low need for behavioral thermoregulation requires further investigation.

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