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RESEARCH ARTICLE

Western Lowland Gorillas (*Gorilla gorilla gorilla*) Change Their Activity Patterns in Response to Frugivory

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The most important environmental factor explaining interspecies variation in ecology and sociality of the great apes is likely to be variation in resource availability. Relatively little is known about the activity patterns of western lowland gorillas (*Gorilla gorilla gorilla*), which inhabit a dramatically different environment from the well-studied mountain gorillas (*G. beringei beringei*). This study aims to provide a detailed quantification of western lowland gorillas' activity budgets using direct observations on one habituated group in Bai Hokou, Central African Republic. We examined how activity patterns of both sexes are shaped by seasonal frugivory. Activity was recorded with 5-min instantaneous sampling between December 2004 and December 2005. During the high-frugivory period the gorillas spent less time feeding and more time traveling than during the low-frugivory period. The silverback spent less time feeding but more time resting than both females and immatures, which likely results from a combination of social and physiological factors. When compared with mountain gorillas, western lowland gorillas spend more time feeding (67 vs. 55%) and traveling (12 vs. 6.5%), but less time resting (21 vs. 34%) and engaging in social/other activities (0.5 vs. 3.6%). This disparity in activity budgets of western lowland gorillas and mountain gorillas may be explained by the more frugivorous diet and the greater dispersion of food resources experienced by western lowland gorillas. Like other apes, western lowland gorillas change their activity patterns in response to changes in the diet. Am. J. Primatol. 71:91–100, 2009. © 2008 Wiley-Liss, Inc.

Key words: western lowland gorillas; activity budget; frugivory; seasonality; sex differences; great apes

INTRODUCTION

Knowledge of inter- and intraspecific variation in activity budgets is important for our understanding of the evolution of sociality and life history patterns in primates. Differences in activity budgets may arise from multiple factors, including body size, digestive capacities, spatial–temporal availability of food resources, and climatic factors [Brockman & van Schaik, 2005; Bronikowski & Altmann, 1996; Dunbar, 1992; Hanya, 2004]. Investigating the behavioral responses of primates to seasonal changes in food availability helps us to understand the mechanisms leading to the diverse adaptations of the apes to different environments.

The great apes are a diverse *taxon* that varies in body size, degree of sexual dimorphism, patterns of sociality, foraging strategies, reproductive parameters, and activity budgets. However, one common characteristic among them is that most great apes face strong seasonal and interannual variation in food availability [Knott, 2005]. Gorillas (*Gorilla* spp.) are the largest living primates and historically have been viewed differently from the other great apes, primarily because of the highly herbaceous diet of the well-studied population, the mountain gorillas (*Gorilla beringei beringei*) of the Virunga Volcanoes. In this unique habitat, fruit availability is extremely low and herbaceous vegetation is highly abundant and available year-round [Watts, 1984, 1998a,b]. In the past decade researchers have emphasized that the majority of gorillas, the western lowland gorillas (*G. gorilla gorilla*), live in areas where herbs occur at lower densities and are more sparsely distributed, whereas fruit may be readily available but with strong seasonal and interannual fluctuations [Doran

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et al., 2002; Tutin & White, 1998]. As a result, western lowland gorillas have a more frugivorous diet than mountain gorillas [reviewed in Doran & McNeilage, 2001; Watts, 1996], though the exact degree of frugivory remains unclear [Doran-Sheehy et al., 2006]. It is clear that such seasonality affects their ranging patterns [e.g. Cipolletta, 2004; Doran-Sheehy et al., 2004; Remis, 1997]. Thus, we cannot assume that mountain gorilla activity budgets are representative of all gorillas.

Although numerous studies on western lowland gorilla behavioral ecology have been initiated in recent decades, most current knowledge comes from indirect observations (feeding trails and fecal analysis) owing to the difficulties of habituating them to human observers [Doran-Sheehy et al., 2007]. The few direct observations of their behavior and activity budgets are based on either a single male [Doran-Sheehy et al., 2006], on semi-habituated groups [Remis, 1994], or on gorillas visiting clearings [e.g. Magliocca & Gautier-Hion, 2002; Parnell, 2002].

The aim of this study is to provide the first detailed account of activity budgets of habituated western lowland gorillas. We also examine how seasonal frugivory and a combination of physiological, physical, and social differences between the sexes may shape the activity patterns in one group of western lowland gorillas.

Frugivory and Seasonality

Many primates respond to seasonal variation in resource availability by showing dietary flexibility and the capacity to switch to lower-energy food when necessary [reviewed in Brockman & van Schaik, 2005]. Large-bodied primates are particularly well suited for these changes in diet, as they have lower energy requirements per unit body weight and a longer hindgut that allows them to extract nutrients by fermenting fibers more efficiently [Lambert, 1998; Milton, 1984]. However, lower-quality diets may require an increase in the time spent feeding and/or traveling, which may affect time invested in other activities such as resting and socializing [Bronikowski & Altmann, 1996; Dunbar, 1992; Overdorff, 1996].

Fruit is generally higher in energy and less fibrous than leaves or herbs but is usually more patchily distributed. Fruit availability is thus expected to influence home-range use, travel distances, feeding time, and social patterns for frugivorous species [Chapman et al., 1994, 1995; Clutton-Brock & Harvey, 1977; Janson & Goldsmith, 1995; White, 1998]. Most great ape species exhibit increases in daily travel distance and/or home-range size as fruit consumption increases [Cipolletta, 2004; Doran, 1997; Doran-Sheehy et al., 2004; Ganas & Robbins, 2005; Goldsmith, 1999; Remis, 1997; Wrangham, 1977; Yamagiwa et al., 2003]. Thus, during the period of high frugivory (HF), we predict that western lowland gorillas will (1) increase their traveling time in order to locate dispersed fruit, (2) reduce the time spent feeding owing to possible higher-energy intake associated with this higher-quality food or, alternatively, the time spent feeding may not vary to compensate for that increased energy spent in the increased travel. During the low-frugivory (LF) period, when relying on a lower-quality diet, we expect (3) western lowland gorillas to spend more time resting to digest more highly fibrous food than during the HF period [Doran, 1997; Dunbar, 1988; Knott, 2005; Williamson & Dunbar, 1999]. Because western lowland gorillas live in an environment where the availability of food resources is more variable in time and space than that of mountain gorillas, we expect western lowland gorillas (4) to spend more time feeding/foraging and traveling than mountain gorillas to meet their nutritional needs, but (5) to spend less time resting as they generally rely on a less fibrous diet.

Age/Sex Differences

Although metabolic rate increases with body weight $(kg)^{0.75}$, the energy required per unit body weight decreases [McNab, 1978]. Thus, immature individuals have higher energetic and nutritional needs than adults [Altmann, 1980] and, among adults, an increased degree of sexual size dimorphism can have significant energetic consequences [Key & Ross, 1999], often resulting in differences in activity patterns among age/sex classes, as observed in mountain gorillas [Watts, 1988]. When sexual size dimorphism is reduced, males and females exhibit greater differentiation in diet than in activity budgets. For example, chimpanzee females forage more on insects and nuts than males, who spend more time cooperatively hunting [e.g. Boesch, 1994; Boesch & Boesch, 1990].

However, other factors can also lead to sex differences in activities. The cost of gestation and lactation may increase the nutritional requirements of females with consequences for their activity budgets [Altmann, 1980; Fox et al., 2004; Knott, 1998, 2001; Takahashi, 2002]. The energy necessary to meet the reproductive costs for females can vary even within the same species in different environmental conditions [Altmann & Alberts, 2005]. Additionally, in group living primates, the need to maintain group cohesion may constrain the foraging patterns of one sex [Key & Ross, 1999], especially when food resources are patchily distributed, and/or the subordinate sex or individuals may need to feed longer (on lower-quality foods) than the dominant ones [Foster & Janson, 1985]. In gorillas, large dominant males may potentially exclude females from preferred food patches [Watts, 1985, personal observation] or, on the contrary, be limited in their ability to reach arboreal feeding sites owing to their large body mass [Doran, 1993; Remis, 1995]. Furthermore, male–male competition, courtship, and mate guarding are energetically costly and time-consuming activities for primate males [Alberts et al., 1996]. Monitoring for predators and infanticidal males potentially may constrain the time they have available for other activities.

As gorillas are highly sexually dimorphic with respect to their body size [Breuer et al., 2007; Smith & Jungers, 1997], sex differences in nutritional requirements and activity budgets are expected. Although male mountain gorillas spend more time feeding than females, the disparity is less than that would be predicted based on the degree of body size dimorphism and may be owing to the costs incurred by lactation and gestation for females [Watts, 1988]. Such sex-specific differences may also occur in western lowland gorillas, although other factors may obfuscate this pattern. Female western lowland gorillas likely experience greater reproductive costs than mountain gorilla females as a result of longer periods of maternal care [Nowell & Fletcher, 2007]. In general, immature individuals must meet the additional costs of growth such that they may need to ingest a greater amount of food than that based on their weight alone. Therefore, in lowland forests, female and immature gorillas may need to spend more time feeding in comparison with mountain gorilla individuals of the same sex–age classes and thus they may spend the same amount of time feeding as adult males despite the large size dimorphism. This study aims to shed light on this issue by providing the first description of sex differences in activity budget of habituated western lowland gorillas.

METHODS

Research was conducted at Bai Hokou located in the Dzanga sector of the Dzanga-Ndoki National Park (1,222 km^2), in south-western Central African Republic (CAR), directed by the Dzanga-Sangha Project [Carroll, 1996]. The climate shows marked seasonal variation in rainfall: the dry season is typically from December to February, when rainfall is less than 80 mm per month. September and October are generally the rainiest months and no clear short dry season is observed (Bai Hokou long-term data). Annual rainfall in 2005 was 1,773 mm. All research below adhered to the protocols and legal requirements in CAR.

Study Group and Data Sampling

Data on activity budgets were collected by S. M., from December 2004 to April 2005, and from June 2005 to December 2005, during half days and occasionally full days of observations ($N_{\text{days}} = 237$, average $h_{\text{obs.}}/\text{day} = 5$). The study group, Makumba, consisted of one silverback, four adult females, one subadult male, three juveniles, and four infants for the entire study. The gorillas accepted human observers at an average distance of 10–13 m, but the silverback and immatures frequently approached observers to a closer distance. We avoided approaching the gorillas very closely in thick vegetation, such as Marantaceae (fam.) patches where visibility was sometimes less than 1 m. Instantaneous scan sampling at 5-min intervals [Altmann, 1974] was used to record the activity and the food eaten by each individual in view (excluding infants) and by the group as a whole. Modifying Watts [1988], activity was classified into four main categories: feeding (including foraging, food processing, chewing), traveling (walking, running, climbing, not related directly with foraging), resting (stationary, sitting down, sleeping, autogrooming), social/other (any social interaction within and between groups, loud vocalizations, playing, vigilant surveillance). Knowledgeable Ba'Aka pygmy trackers helped to identify plants consumed by gorillas. At each scan, the group activity, besides individual activity, was recorded as the activity performed by the majority of individuals in view. In rare cases in which an equal number of individuals in sight were engaged in two different activities, feeding was recorded preferentially over traveling and resting, and traveling over the latter. When the same situation occurred again at the next scan the other activity (e.g. different from feeding) was recorded.

The gorillas were active from approximately 6:15–6:30 a.m. to 5:30–6:00 p.m. Owing to the danger of meeting elephants at dawn and dusk, the start and end time of the observations varied with distance of the group from the camp. However, we restricted the data set to the period between 7:00 a.m. and 5:15 p.m. for consistency. The total amount of visual observation time was 720 hr ($N_{\text{group scans}} = 8{,}637$). On average, three individuals were observed per scan; thus, the individual data sets are not of equal size. The silverback was generally more vocal and was thus easier to detect than females and immatures, especially while taking part in activities other than feeding. This resulted in a largest sample size for the silverback ($N_{\text{Scans}} = 5{,}254$) in comparison with all other individuals (average females $N_{\text{Scans}} = 1{,}414$ and average immatures $N_{\text{Scans}} = 1{,}690$).

For all statistical analyses we considered the daily percentage (or number of scans per day) of each activity (per each individual or for the group) in each season as a single independent data point. These data were found to be temporally independent by linear autocorrelation tests, based on Spearman's rank correlation [Bortz et al., 1990], when tested separately for each combination of activity and season. Days with less than 1 hr of observation were excluded from the analysis; thus, the actual sample size was $N_{\text{group scans}} = 5{,}786$. Days with one or more hours of observation represent the gorilla activity

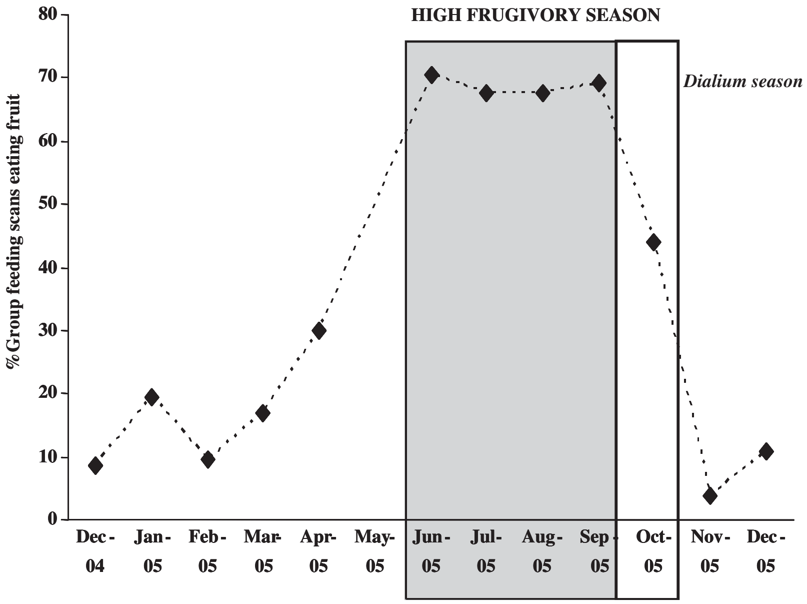

Fig. 1. Fruit consumption from group feeding scans. The large shaded part indicates the high-frugivory (HF) season and the other months constitute the low-frugivory (LF) season except October 2005, which was a *Dialium* season (see ''Seasonal subdivision and statistical methods'').

budget as well as days with longer observation, as shown by accumulation graphs of the number of scans per day against daily percentage of each activity. The only exception was traveling, which was a rare activity and may have been overestimated in days with few data points.

Seasonal Subdivision and Statistical Methods

To test for seasonal differences in the activity patterns of the gorillas, we divided the study period into two: (a) the HF season, from June to September 2005, which includes all months when approximately 70% of the group feeding scans were fruit consumption and corresponds to higher fruit availability [Masi, 2008]; and (b) the LF season from December 2004 to April 2005 and November to December 2005 (Fig. 1). October 2005 was characterized by an intermediate level of frugivory (Fig. 1) owing to fruiting of *Dialium* spp. (81% of gorilla fruit consumption for this month), which does not happen each year [Cipolletta, personal observation]. Because it was an exceptional year for this fruit species, we felt justified in excluding this month from the analysis so that we could focus on the differences between obviously HF and LF months. Furthermore, the fruit months were typically characterized by the availability and consumption of a large variety of fruits, whereas October 2005 was characterized just by this one fruit species.

To investigate if there were seasonal differences for each activity we used Wilcoxon exact tests based on averages per season using each individual as an independent data point. As individuals are part of a group, they may not be totally independent; however, this was the best way to conduct statistical analysis and to account for the inherent limitation of conducting statistics on data from social animals.

To test for differences between sex and age classes in activity budgets in the two seasonal periods, we used a permutation test that is able to cope with related samples (repeated measures) with missing values [Mundry, 1999]. In principle, such an analysis would be done using a single multifactor general linear model but the use of more traditional statistical methods was not suitable for several reasons: (1) the data set had a large proportion of missing values owing to the fact that not every individual was observed regularly (i.e. daily), (2) the data contained many zeroes, and (3) the data were also clearly not normally distributed and had heterogeneous error variances. Permutation tests can cope with such data as the sampling distribution is derived from repeated randomization of the data itself [Manly, 1997]. We randomly assigned frequencies of the activities to the different individuals observed. To account for the related nature of the samples (i.e. several individuals observed on the same day) randomization took place only within days. This procedure was repeated many times, and hence derived the frequency distribution of differences between individuals as expected given the null hypothesis (i.e. no differences between individuals). In one case the P-value of 1,000 permutation analysis was close to the critical threshold of significance ($P = 0.055$) and the test was repeated with 10,000 and 100,000 permutations to confirm this tendency. This permutation test includes a post hoc procedure comparing between subjects.

TABLE I. Activity Budget of the Study Group and Comparison of Different Populations of Gorillas and Great Apes

Species	Study site	Study animals	Habituation	% Feeding	% Resting	% Traveling	% Social/ Other
Gorilla gorilla gorilla	Bai Hokou[a]	1 Group (13)	Yes	67.1	21	11.7	0.5
Gorilla gorilla gorilla	Bai Hokou[b]	? Groups (?)	Semi-	54.5	28	13	0
Gorilla gorilla gorilla	Maya Nord[c]	37 Groups, 21 solitary males	*Bai* study	72	0	16.5	11.5
Gorilla beringei beringei	Karisoke[d]	4 Groups (20)	Yes	55.4	34.4	6.5	3.6
Pongo pygmaeus albelii	Suaq Balimbing[e]	41 Individuals	Yes	55	25	17	3
Pongo pygmaeus pygmaeus	Kutai[f]	8 Individuals	Yes	43.9	45.9	9.5	1
Pan troglodytes verus	Tai[g]	1 Community (70)	Yes	43	39	12	6
Pan troglodytes verus	Tai[h]	1 Community (79)	Yes	54	22.0[i]	22	In resting
Pan troglodytes troglodytes	Goualougo Triangle[j]	1 Community (54)	Yes	22.1	50.8	12.8	14.3
Pan troglodytes schweinfurthii	Budongo[k]	1 Community (56)	Semi-	52.7	25	7.5	14.3
Pan troglodytes schweinfurthii	Gombe[l]	1 Community (14 males)	Yes	55.6	23.5	14.2	6.2[m]
Pan troglodytes schweinfurthii	Gombe[n]	1 Community (31)	Yes	42.8	18.9	13.4	24.9
Pan troglodytes schweinfurthii	Mahale[o]	1 Community (100)	Yes	29.7	38.6[i]	19.5	12.0[m]
Pan paniscus	Lomako[p]	Not provided	Yes[q]	40.4	16.1	31.9	6.3

The Study animals column indicates the number of social units per each study and the number of individuals per social unit in parentheses.

[a] This study.

[b] Remis [1994]: percentages obtained as mean of females and group male overall activity budget.

[c] Magliocca and Gautier-Hion [2002]: Social/Other is the sum of visual surveillance, social behavior, miscellaneous, and water consumption.

[d] Watts [1988].

[e] Fox et al. [2004].

[f] Mitani [1989].

[g] Doran [1997].

[h] Boesch and Boesch-Achermann [2000]: feeding includes meat eating.

[i] Inclusive of social interactions.

[j] Sanz [2004]: data from ‘‘all individuals’’ and ‘‘group scan observations.’’

[k] Fawcett [2000].

[l] Wrangham [1977]: percentages are the mean of the activity budgets in the three different habitats, excluding the ‘‘camp.’’

[m] Only grooming.

[n] Teleki [1981].

[o] Huffman [1990]: percentages are the mean of the activity budgets of the individuals of different age–sex classes.

[p] White [1992].

[q] Not fully habituated.

RESULTS

The group spent most of its time feeding (67.1%), followed by resting (21.0%) and traveling (11.7%). Very little time (0.5%) was devoted to social/other activities (Table I). Hooting, a long distance call used by the gorillas for calling group members or while interacting with other social units, made up the highest proportion of the ‘‘social/other’’ (95.0%). Grooming was never observed except for mothers grooming infants less than 2 years old (16.3 % of the ‘‘social/other’’ from female scans).

Fruit Consumption and Seasonal Variation in Activity Budget

There was monthly variation in the time the group spent feeding with the maximum being from December 2004 to March 2005, decreasing from April to August 2005, and increasing again in September and October 2005 (linear autocorrelation with a lag equaling 1 month: $r_s = 0.779$, $N = 12$, $P = 0.012$; Fig. 2a). Time spent resting tended to vary monthly ($r_s = 0.571$, $N = 12$, $P = 0.083$) and inversely to the amount of time spent feeding. The group also showed significant monthly variation in time spent traveling ($r_s = 0.678$, $N = 12$, $P = 0.024$). They spent the least amount of time traveling from December 2004 to March 2005. As fruit became a larger proportion of their diet (June–September 2005), the time spent traveling increased.

Fruit consumption varied over time, and reached approximately 70% of feeding scans from June to September 2005 (Fig. 1), with corresponding variation in the gorillas' activity budget. As expected during the HF season the gorillas spent significantly less time feeding, and more time traveling (for both: Wilcoxon exact test, $T^{+} = 45$, $N = 9$, $P = 0.004$), than during the LF season. Contrary to our prediction, the

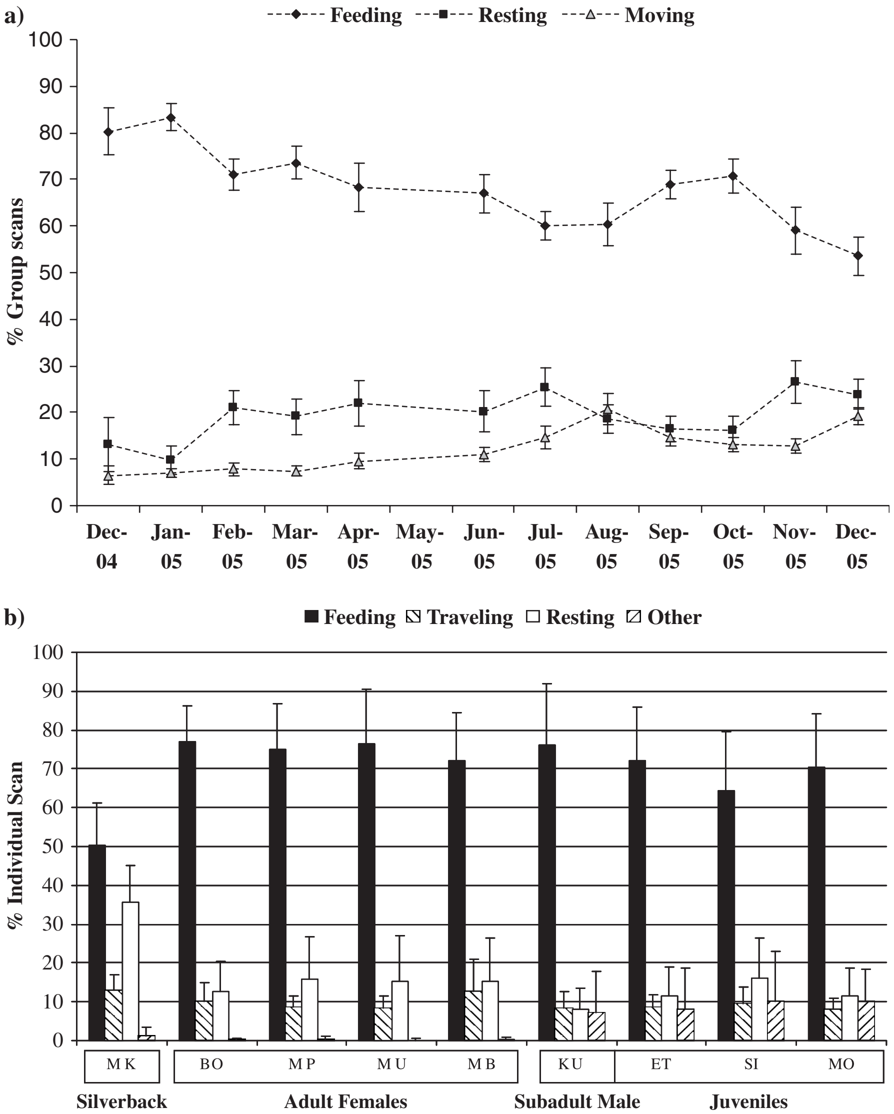

Fig. 2. Mean activity budget (**a**) of the study group as a whole, and (**b**) of individuals in different age–sex classes. Adult females' reproductive status: BO was pregnant for the last 3 months of the study, MP and MU were lactating (1–2 year old infants), MB was pregnant for the last 7 months of the study.

time spent resting and in social/other activities did not differ significantly between the two periods ($T^+ = 37$, $N = 9$, $P = 0.097$; $T^+ = 36$, $N = 9$, $P = 0.129$).

Age/Sex Variation in Activity Budgets

There was variation in activity budgets among the age and sex classes (Fig. 2b), with the silverback spending less time feeding in both seasons (HF = 46.7%, LF = 51.7%) than the adult females (HF = 65.4%, LF = 80.3%) and immatures (HF = 61.1%, LF = 76.1%; for statistical results of permutation test for related samples, see Table II). Concurrently, the silverback rested more (HF = 36.2%, LF = 33.2%) than adult females (HF = 21.1%, LF = 10.5%) and immatures (HF = 11.1%, LF = 12.3%), though during the HF season the differences between the male and females were weaker. The silverback spent more time traveling (HF = 16.9%, LF = 12.9%) than both the females (HF = 13.4%, LF = 9.1%) and immatures (HF = 11.4%, LF = 9.0%) but the differences were significant only with immatures during the HF season (Table II). Immatures spent more time (16.5%) than the silverback (0.2%) in social/other activities during the HF season. The most common social activity of the immatures was playing (range: 95–99% of scans of social/other activities), which occurred more during the HF season (4% of total immature activities in HF vs. 1% in LF) as would be predicted by the assumed higher sugar intake gained when eating fruit [Barrett et al., 1992].

TABLE II. Results of Permutation Analysis Testing for Individual Differences in Activity Budgets Within Each Seasonal Period Comparing the Silverback (SB) With Adult Females (AFs) and With Immatures (IMs)

		SB-AFs ($N = 5$)		SB-AF		AF-AF				
Season	Activity	$\lvert D_{tot}\rvert$	P	Smallest $\lvert D_{pw}\rvert$	n. $P \leq 0.05$	Largest $\lvert D_{pw}\rvert$	n. $P \leq 0.05$		Days	N
Low frugivory	Feeding	131.45	0.001	25.44	4	5.65	0	Low frugivory	114	358
High frugivory	Feeding	96.43	0.007	12.15	4	8.52	0	High frugivory	70	222
Low frugivory	Resting	105.44	0.001	20.82	4	4.64	0			
High frugivory	Resting	77.14	0.053*	12.85	4	5.35	0			
Low frugivory	Traveling	24.25	0.092	2.01	3	2.57	0			
High frugivory	Traveling	36.50	0.197	1.09	0	6.97	0			
Low frugivory	Other	9.19	0.014	2.06	4	0.48	0			
High frugivory	Other	1.72	0.837	0.00	0	0.39	0			
		SB-IMs ($N = 5$)		SB-IM		IM-IM				
Low frugivory	Feeding	156.01	0.001	15.21	4	16.66	3	Low frugivory	115	419
High frugivory	Feeding	81.42	0.009	10.88	4	6.45	0	High frugivory	60	235
Low frugivory	Resting	137.75	0.001	12.80	4	14.54	3			
High frugivory	Resting	125.29	0.001	23.67	4	5.34	0			
Low frugivory	Traveling	22.01	0.16	2.71	2	2.32	0			
High frugivory	Traveling	33.48	0.014	1.37	2	5.06	1			
Low frugivory	Other	18.58	0.018	0.30	0	2.60	2			
High frugivory	Other	83.84	0.001	14.16	4	5.57	0			

See text for an explanation of methods. The columns SB-AF, AF-AF, SB-IM, and IM-IM summarize the post hoc comparisons between the age–sex classes, procedure included in the permutation test [Mundry, 1999]. In Activity column, Other includes "social/other" activities; D_{tot}, sum of absolute differences between mean entries per subject (test statistic of the permutation test); D_{pw}, pair-wise difference between average entries per subject; n. $P \leq 0.05$, number of P-values smaller or equal to 0.05; Days, number of days of observation; N, number of entries in the analysis as the product of number of days and subjects observed minus the number of missing values. *P-value based on 100,000 permutations.

The four females of the study group did not differ from one another in their activity budgets (Table II; Fig. 2b). The immatures differed from each other in the time spent feeding and resting in the LF season (Table II; Fig. 2b). The subadult (KU, male, 6–7 years old) spent more time feeding and less resting than juveniles, accounting for four out of the nine significant post hoc tests when comparing between immatures (Table II). No differences were found in the time females and immatures spent feeding or traveling ($U_{\text{range}} = 2$–8, $N_{\text{females}} = N_{\text{immatures}} = 4$, $P_{\text{range}} = 0.114$–1). The immatures spent more time in social/other activities (HF = 2.5%, LF = 16.5%) than females (HF = 0.2%, LF = 0.1%; both seasons: $U = 0$, $N_{\text{females}} = N_{\text{immatures}} = 4$, $P_{\text{e}} = 0.029$) and rested less during the HF season (females 21.1%, immatures 11.1%; $U = 0$, $N_{\text{females}} = N_{\text{immatures}} = 4$, $P_{\text{e}} = 0.029$) as they were often playing when adults were resting. No differences were found for any other combination of activity and season ($U_{\text{range}} = 2$–8, $N_{\text{females}} = N_{\text{immatures}} = 4$, $P_{\text{range}} = 0.114$–1).

DISCUSSION

Fruit Consumption and Seasonal Influence

Western lowland gorillas respond to seasonal variation in resource availability by altering their diet [Rogers et al., 2004] and consequently adjusting their activity pattern as do other primates [e.g. Doran, 1997; Knott, 2005; Overdorff, 1996]. As expected, gorillas spent less time feeding during the HF season, which may be related to the greater energy gained from fruit. Contrary to predictions, the time spent resting tended to increase during the HF season. During this period, the gorillas also spent more time traveling, which is consistent with previous observations of longer daily journey length when gorillas increase fruit consumption, which is likely a consequence of the patchy distribution of fruit [e.g. Cipolletta, 2004; Doran-Sheehy et al., 2004; Ganas & Robbins, 2005; Goldsmith, 1999; Remis, 1997].

Age/Sex Differences

As for several other primate species [Clutton-Brock, 1977; Fox et al., 2004; Mitani, 1989], the adult male in this study spent less time feeding and more time resting than females and immatures. There are several reasons why such age/sex differences may occur: (1) the reproductive status of females may lead to higher feeding times owing to the extra energetic costs associated with pregnancy and lactation; immatures may need to meet the costs of growth [e.g. Altmann, 1980; Clutton-Brock, 1977; Fox et al., 2004; Harcourt & Stewart, 1984; Key & Ross, 1999]; (2) male dominance may allow males to displace females or immatures from preferred feeding sites [Dittus, 1979; Masi, personal observation; Remis, 1995], generating differences in food-intake rates and thus activity budgets [Clutton-Brock, 1977]; that is, when fruit is a monopolizable resource, females excluded from feeding sites may need to spend more time feeding on lower-quality foods to meet their nutritional needs, and may also need to travel more searching for alternative food source; (3) male dominance for food resources may allow males to invest more time monitoring the environment for predators, and maintaining group cohesion to help guard against infanticidal rival males and/or female transfers [Doran & McNeilage, 2001]. In fact, western lowland gorilla females are often observed feeding several hundred meters away from the group [Masi, unpublished data]. In addition, observations of the group's silverback walking with food in his hands to reach the group, and waiting for individuals left behind (recorded here as resting), illustrate how promoting group cohesion may affect silverback activity budget.

Among the great apes, the pattern of males feeding more than females has only been consistently observed in mountain gorillas [Watts, 1988]. However, given that the differences in time spent feeding are proportionally smaller than the differences in body size, the reproductive costs for female gorillas may balance out the costs of maintaining the larger size of males. The results of this study suggest that the greater unpredictability of food availability in the lowland forest and the longer period of maternal care in comparison with mountain gorillas [Nowell & Fletcher, 2007] generate greater costs of reproduction for females and of growth for immatures in western lowland gorillas. This explains why females and immature spend more time feeding than does the silverback.

Comparison With Mountain Gorillas and Other Apes

Differences in resource availability are likely a significant environmental factor explaining interspecies variation in activity budgets, feeding ecology, and great ape socioecology [Brockman & van Schaik, 2005; Sterck et al., 1997; van Schaik, 1989; Wrangham, 1979]. For example, the extreme unpredictability of fruit production in the forests of Borneo puts constraints on orangutan activity budgets differently than the rest of the apes including the western lowland gorillas; when fruit is abundant they increase time spent feeding [Knott, 1998, 2005]. At the other extreme, a paucity of fruit trees and an unusually high availability of herbaceous vegetation in the Virunga Volcanoes promote the highly terrestrial folivore diet of mountain gorillas, which experience little seasonality in activity budgets and spend less time traveling compared with other apes [Watts, 1996].

The results from this study differ slightly from previous studies on western lowland gorillas carried out in Bai Hokou and in forest clearings [e.g. Magliocca & Gautier-Hion, 2002; Remis, 1994]. In both cases, gorillas were only observed part of the time, either because they were semi-habituated or because observations were made in a specific habitat, essentially a large feeding patch. Compared with mountain gorillas, western lowland gorillas invest more time feeding (67 vs. 55%) and traveling (12 vs. 6.5%), probably because of the patchy distribution of herbs, unpredictable fruit availability, and increased travel costs. Mountain gorillas may also need to invest more time resting than western lowland gorillas (34 vs. 21%), in order to ferment fibers and extract nutrients from a more fibrous diet [Dasilva, 1992; Dunbar, 1988; Smith, 1977]. The greater amount of time spent resting might explain the greater amount of time they spend socializing, but less time spent resting by western lowland gorillas cannot explain the absence of grooming behavior observed in this species. The hooting vocalization was the most common record in the social/other activities, but is rarely used by mountain gorillas [Robbins, personal observation]. This difference may be owing to the lower group cohesion in western lowland gorillas, which requires greater communication for movement coordination and location of group members and/or other social units.

As the largest extant primate, western lowland gorillas may need to spend more time feeding than other apes to meet the greater nutritional requirements. Nevertheless, the patchy food distribution may be responsible for western lowland gorillas spending approximately the same time traveling as other apes, which may constrain the time available for resting and social activities. However, some caution should be taken when making comparisons between studies, as activity budget depends on the size of the study groups and different definitions may lead to dramatic changes in results [Dunbar, 1988; Watts, 1988].

In conclusion, because resource availability and foraging strategies differ dramatically among gorillas found in lowland and montane habitats [reviewed in Robbins, 2007], it is not surprising that their activity patterns vary. This study sheds light on the relationship between food availability and activity budgets of western lowland gorillas, but additional studies of their behavior are needed to better understand their socioecology and how they differ from the other great apes.

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