

## RESEARCH ARTICLES

### Environmental Influences on Mountain Gorilla Time Budgets

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Data on the time budgets of mountain gorillas (*Gorilla gorilla beringei*) were collected during field studies in the Virunga Volcanoes region of Rwanda and Zaire. Focal sampling was used to determine the proportion of time that individuals of different age/sex classes spent in several mutually exclusive activity states. The gorillas spent the majority of daylight hours feeding; most of the rest of the day was devoted to resting, with little time spent moving or engaged in social activity. The time budget varied among the different subhabitats used by the gorillas, and the gorillas satisfied subsistence needs more quickly when in areas where food was more abundant and/or of better nutritional quality. Silverbacks spent more time feeding than all other age/sex classes, but age/sex class differences were not great. All age/sex classes responded to variability in habitat quality in similar fashion. Unlike the case for many other primates, there was no significant seasonal variation in time budgets. There was a direct relationship between group size and time spent feeding, although variation in relation to group size was lower than that in relation to variation in habitat quality. These results are consistent with the relationship of feeding time to body size in primates. They are also consistent with other evidence that social foraging entails a cost to gorilla females, but that this cost is low in comparison to those faced by many other primates. Permanent association with males apparently offers little ecological disadvantage to females, who are likely to be more than compensated by mutualistic benefits.

**Key words:** gorillas, time budgets, habitat quality, male-female association, feeding, activity

#### INTRODUCTION

The way in which animals distribute time among various activities has important consequences for survival and reproduction. Many ecological and social factors can constrain time budgets. For example, time spent feeding can be influenced by body size, digestive physiology, and diet quality [Janis, 1976; Clutton-Brock & Harvey, 1977]; by spatial and temporal variability in habitat

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quality and climate [Post, 1981; Clutton-Brock et al., 1982; Iwamoto & Dunbar, 1983]; by the nutritional demands of reproduction [Altmann, 1980, 1983]; and by group size [Slatkin & Hausfater, 1976; Caraco, 1979; Barnard, 1980; Barnard et al., 1983; van Schaik et al., 1983]. The effects of one factor may not be universally the same; for example, in larger groups individuals may have to feed longer because of increased competition [baboons: Slatkin & Hausfater, 1976; Stacey, 1986; house sparrows: Barnard, 1980; long-tailed macaques: van Schaik et al., 1983], or they may feed more efficiently because their need for vigilance against predators is relaxed [juncos: Caraco, 1979; mixed species flocks of shorebirds: Barnard et al., 1983].

Demands on time can conflict, sometimes in a manner that shows the importance of having time for nonsubsistence activities ["free time"; Kiester & Slatkin, 1974]. Animals as diverse as waterbuck [Spinage, 1968], impala [Jarman & Jarman, 1973], feral horses [Duncan, 1980], and red deer [Clutton-Brock et al., 1982] appropriate extra time for reproductive activities from feeding, not resting. Giant panda time budgets reflect the need of herbivores with the gut of a carnivore to conserve energy [Schaller et al., 1985]. The duration of nursing by female yellow baboons is constrained by the need to devote time to resting and social activity [Altmann, 1980, 1983].

Sociality can have a competitive cost that is manifested in part in effects on activity scheduling, such as the positive relationship between group size and feeding time in cases mentioned above. These costs can differ between males and females, with the consequence that optimal social dispersion patterns are different for the two sexes [Wrangham, 1979, 1982]. For the great apes, it has been argued that foraging in association with males can lead to problems in the scheduling of activities and impose nutritional burdens that limit female gregariousness in the case of chimpanzees and make it impossible in the case of orangutans [Wrangham, 1979; Wrangham & Smuts, 1980; Rodman, 1979, 1985]. Gorillas, however, forage in cohesive groups in which females associate with a male or males despite some cost, at least in mountain gorillas (*Gorilla gorilla beringei*), to social foraging [Watts, 1985]. Mountain gorillas are large folivores. The vegetational composition of their habitat varies on a scale that is large relative to the animals' daily movements, and although this is associated with some variation in food abundance and quality, their food supply varies less in space and time than do those of the other great apes [Watts, 1983, 1984; Vedder, 1984].

Early data on mountain gorilla time budgets [Fossey & Harcourt, 1977] was discordant with both theoretical expectations and empirical data from other primates with regard to the influence of body size on time spent feeding [Clutton-Brock & Harvey, 1977]. A recent restudy [Harcourt & Stewart, 1984] removed this anomaly, which apparently was a methodological artifact [ibid.; Watts, 1983]. It remains unanswered, however, to what extent mountain gorilla activity patterns are influenced by characteristics of their food supply and other ecological factors and whether any ecological constraints act differently on males and females. In this paper, more detailed data on mountain gorilla time budgets than previously available are presented. These data are used to examine spatial and seasonal variation and sex differences in time use, and to consider the implications of this variation for the relative advantages of permanent male/female association.

## STUDY SITE

Most of the data presented here were collected during a 17-month field study of mountain gorilla behavioral ecology in 1978–79 in Rwanda's Parc National des Volcans and the adjacent Parc des Virungas of Zaire. These are supplemented with

some data collected during another 17 month field study in 1984–85. Observations were made from a base at the Karisoke Research Centre.

The study site is a 25-km<sup>2</sup> area of montane tropical moist forest that extends in altitude from 2,600 to 3,700 m. Annual rainfall is about 1,700 mm. There is a long rainy season from September through January, a short rainy season from March through May, a dry season from June through August, and a variable inter-rains period around January or February. The mean maximum daily temperature at 3,000 m was 14.8°C in 1978–79; the mean minimum was 3.8°C.

Detailed description of the vegetation can be found in Schaller [1963], Spinage [1972], Fossey & Harcourt [1977], Vedder [1984], and Watts [1984]. The predominant cover is *Hagenia-Hypericum* woodland with a very dense herbaceous understory. Stem density and species composition in the understory vary with topography, altitude, canopy cover, and other factors. Nearly all of the gorillas' diet consists of foliage from understory herbs and vines [Fossey & Harcourt, 1977; Watts, 1984]. Other altitudinally and/or topographically restricted vegetation types also occur, such as afro-alpine vegetation at high altitudes and bamboo forest at the lower edge of the study area. The gorillas' habitat can be divided into a number of vegetation zones [Fossey & Harcourt, 1977; Vedder, 1984; Watts, 1984]. Visits by the gorillas to a given zone can last from several minutes to a week or more [Watts, 1983].

## MATERIALS AND METHODS

### Time Budget Analysis

Data come from four social groups (Karisoke Groups 4, Pn, 5, and Nk), with most of the data from Group 4. Focal sampling [Altmann, 1974] was used to collect time budget data on individuals of all age/sex classes other than infants. Total sample time for the analyses below was about 2,400 hours. Numbers of individuals in each age/sex class that contributed data were silverbacks, 4; adult females, 9 (including two post-menarcheal but apparently not yet fertile young adults); blackbacks, 3; juveniles, 4.

During each sample, the absolute amount of time that the focal individual spent in each of five mutually exclusive activity states was recorded. The states are listed below:

1. Feeding: preparation and ingestion of food. Feeding bouts began when a stationary individual, either on arrival at a feeding spot or after having engaged in some other activity there for at least 5 seconds, started to prepare food for ingestion (which included chewing). They ended when the individual ceased preparation and ingestion for at least five seconds or shifted position by at least 1 m. Feeding time is referred to below as " $T_{\text{feed}}$ ."

2. Moving: all locomotor activity other than shifts of position of less than 1 m during feeding and resting and locomotion during play. This time is referred to below as " $T_{\text{move}}$ ."

3. Resting: stationary, nonsocial behavior during which animals were not feeding (sleeping, autogrooming, etc.). This time is referred to below as " $T_{\text{rest}}$ ."

4. Social: social interactions with a measurable duration, including play, allogrooming, sexual behavior, and some forms of agonistic behavior. This is referred to below as " $T_{\text{social}}$ ."

5. Other: other subsistence behavior, including nest building and, for females, nursing. Because it was usually impossible to be certain whether a female was nursing when she had her back turned, and because "other" activities occupied only a tiny fraction of observation time, they are not discussed below.

“Foraging time” ( $T_{\text{forage}}$ ) is defined as the sum of feeding and moving time. (Most locomotion occurred during discrete feeding periods and appeared to be associated with feeding.) All remaining time is “free time” ( $T_{\text{free}}$ ).

Focal samples were not all-day follows, nor were samples distributed equally among all hours of the day. Equal weight was given to each hour in data analysis to correct for any bias that arose from diurnal variation in activity patterns by

1. Calculating the proportion of time spent in each activity state by the focal animal during each hour of the sample.

2. Pooling these data by age/sex class and calculating mean values for the percentage of time spent in each activity state by the focal animal during each hour from 0600 to 1800 hours by members of each class.

3. Calculating the mean of these proportions over all hours of the day to obtain the average proportion of time that a member of that class devoted to each activity per day. Steps 2 and 3 were also performed for each individual for whom sample time was reasonably long.

An aggregate Group 4 time budget was calculated by weighting the results from step 3 according to the following formula, modified from Marsh [1981]:  $P_n = \sum_{i=1}^n P_i \cdot M_i$  where  $P_n$  is the percentage of the aggregate time budget spent in each activity state,  $n$  is the number of age/sex classes,  $P_i$  is the percentage of time spent by members of age/sex class  $i$  in activity state  $p$ , and  $M_i$  is the percentage representation of class  $i$  in the group.  $M_i$  was varied to take into account demographic changes.

These analyses were repeated with the data partitioned by the vegetation zone in which observations were made or by month or season. These were considered separate cases for statistical purposes.

The distance that focal individuals moved between each pair of consecutively used feeding spots was estimated, and bite rates for different foods were counted opportunistically. Data on food intake rate and on total food intake per day were gathered during focal samples of individual feeding behavior; the methodology is described in Watts [1984].

## **Vegetation Analysis**

The seven vegetation zones considered in analyses below and methods used to measure the density, frequency (percentage occurrence at 1-m<sup>2</sup> spots) and biomass of gorilla food plant species within them, are described in Watts [1984]. Data on the nutritional content of gorilla food plants [Watts, 1983; Waterman et al., 1983] were used to estimate mean nutrient availability per m<sup>2</sup> within each vegetation zone. Density data for all food species combined were used to calculate an index of dispersion [Shimwell, 1971] within each zone; this is a measure of the degree to which food resources are clumped. Measures of diet quality within zones and of food distribution and abundance used here are given in Table I.

## **RESULTS**

### **Overall Time Budget**

Feeding occupied the majority (55.4%) of an average 12-hour day, and resting (34.4%) accounted for most of the remainder. The gorillas spent little time moving (6.5%). They also spent little time engaged in social interaction (3.6%); this reflects the paucity of social interactions among many individuals [Harcourt, 1979a,b].

TABLE I. Measures of Food Distribution and Quality and of Diet Quality Within Vegetation Zones and of Zone Use by Group 4

Measure	Vegetation zone						
	Nettles	Saddle	Herbaceous slope	Giant lobelia/thistle	Brush/ridge	Lobelia	Afro-alpine
Stem density	18.5	8.9	12.2	4.6	2.9	1.6	0.9
% Frequency of food sources	98.0	94.3	99.0	71.8	76.4	45.8	33.3
Index of dispersion	5.4	7.3	5.2	2.9	3.3	2.8	2.0
Herbaceous food biomass, g/m <sup>2</sup>	1,207	799	1,650	1,220	568	73	27
<i>G. ruwenzoriense</i> biomass, g/m <sup>2</sup>	115	70	75	24	46	17	0.5
Protein biomass gr/m <sup>2</sup>	17.6	10.6	19.0	11.1	6.9	2.3	1.1
% Digestibility of diet	68.1	66.4	65.0	67.0	63.3	55.5	48.6
Dietary protein % wet weight	2.19	2.04	2.04	2.39	2.68	2.7	1.59
% Use of zone	17.9	16.9	38.2	14.7	9.1	4.6	3.2
Intensity of zone use	1.52	0.41	1.65	2.97	0.99	0.62	0.43

### Variation Among Vegetation Zones

Activity proportions in different vegetation zones (Table II) varied significantly (Friedman 2-way analyses of variance with each age/sex class treated as a different case:  $X^2 = 23.57$ ;  $df = 3$ ;  $P < 0.001$  for  $T_{\text{feed}}$ ;  $X^2 = 22.92$ ;  $df = 3$ ;  $P < 0.001$  for  $T_{\text{move}}$ ;  $X^2 = 22.73$ ;  $df = 3$ ;  $P < 0.001$  for  $T_{\text{rest}}$ ;  $X^2 = 12.50$ ;  $df = 3$ ;  $P < 0.01$  for  $T_{\text{social}}$ ). The direction of variation was consistent among age/sex classes. The afro-alpine zone stands out:  $T_{\text{feed}}$  was very high and  $T_{\text{move}}$  relatively high there, while  $T_{\text{rest}}$  and  $T_{\text{social}}$  were very low. Observations in this zone covered only the interval 0800–1700 hours, but it is unlikely that the absence of earlier morning and later afternoon data introduced a major bias because these were usually times of intensive feeding. The gorillas foraged almost continuously when in this zone and never rested for the prolonged periods that typically followed intensive feeding at lower altitudes. They usually spent only part of a day, and rarely more than 24 hours, in this zone per visit; the mean duration of 12 visits by Group 4 in 1978–79 was 6 hours.

When the different components of the time budget are correlated across vegetation zones, there are significant ( $P < 0.05$ ) inverse relationships of  $T_{\text{feed}}$  per zone with  $T_{\text{rest}}$ ,  $T_{\text{social}}$ , and  $T_{\text{free}}$ ; of  $T_{\text{move}}$  with  $T_{\text{rest}}$  and  $T_{\text{free}}$ ; and of  $T_{\text{forage}}$  and  $T_{\text{social}}$ . There was a significant positive correlation between  $T_{\text{rest}}$  and  $T_{\text{social}}$ . Values for time spent feeding, moving, and foraging were all highly positively correlated with each other. The exact meaning of these correlations can be unclear because the variables form an interdependent set [Post, 1981], but it is noteworthy that the gorillas both rested and socialized less when in areas where it took them longer to satisfy subsistence needs.

Table III shows correlations of zone-specific activity proportions with various characteristics of the food supply and of diet quality.  $T_{\text{feed}}$  showed significant inverse correlations with the index of food source dispersion, food source frequency, the biomass of herbaceous food per m<sup>2</sup>, the biomass of protein per m<sup>2</sup>, the biomass

TABLE II. Group Time Budgets in Different Vegetation Zones\*

Zone	Activity category				
	Feed	Rest	Move	Social	Other
Nettles	50.0	39.3	5.7	4.7	0.3
Saddle	51.6	36.1	7.1	4.8	0.3
Herbaceous slope	55.3	33.9	6.5	3.9	0.4
Giant lobelia/thistle	56.4	33.0	7.1	3.2	0.3
Brush/ridge	60.3	31.2	6.5	1.6	0.4
Lobelia	64.0	27.3	7.5	1.2	0.4
Afro-alpine	80.1	11.1	7.8	0.7	0.3

\*Data from Group 4 only.

TABLE III. Correlations of Activity Proportions With Habitat and Dietary Variables†

Variable	Activity category					
	Feed	Rest	Move	Social	Forage	Free
Stem density	-0.74	0.70	-0.76*	0.86*	-0.76*	0.76*
Index of dispersion	-0.77*	0.71	-0.56	0.89**	-0.75*	0.76*
% frequency	-0.91**	0.87**	-0.86*	0.91**	-0.92**	-0.92**
Herbaceous food biomass	-0.75*	-0.72	-0.71	0.79*	-0.76*	0.76*
<i>G. ruwenzoriense</i> biomass	-0.81*	0.79*	-0.85*	0.85*	-0.82*	0.83*
Protein biomass	-0.80*	0.77*	-0.79*	0.86**	-0.81*	0.82*
Dietary protein	-0.35	0.45	-0.46	-0.12	-0.36	0.34
Diet digestibility	-0.96**	0.95**	-0.87**	0.86*	-0.96**	0.96**
% zone use	-0.60	0.57	-0.56	0.69	-0.61	0.61
Intensity of zone use	-0.40	0.41	-0.40	0.32	-0.41	0.41

†Data from Group 4 only.

\* $P \leq 0.05$ .

\*\* $P \leq 0.01$ .

of *Galium ruwenzoriense*, and the digestibility of the zone-specific diet. *G. ruwenzoriense* is a high-quality food that is quantitatively the most important in the gorillas' diet [Watts, 1984]. This inverse correlation of  $T_{\text{feed}}$  with food species density approaches significance at  $P < 0.05$ .

The pattern was very similar for  $T_{\text{forage}}$ , except that its inverse correlation with stem density was significant at  $P < 0.05$ .

$T_{\text{move}}$  had significant inverse correlations with stem density, food frequency, *G. ruwenzoriense* biomass, protein biomass, and diet digestibility.

$T_{\text{rest}}$  showed significant positive correlations with food frequency, diet digestibility, *G. ruwenzoriense* biomass, and protein biomass. Positive correlations of  $T_{\text{rest}}$  with herbaceous food biomass, stem density, and food dispersion approached significance at  $P < 0.05$ .

$T_{\text{social}}$  showed significant positive correlations with stem density, food frequency, the index of dispersion, herbaceous food biomass, *G. ruwenzoriense* biomass, protein biomass, and diet digestibility. The pattern for  $T_{\text{free}}$  was identical.

Mountain gorillas selectively feed on foods (such as *G. ruwenzoriense*) that are high in protein and highly digestible [Watts, 1983]. On this basis, areas where the abundance of foods rich in protein and easily digestible is high and where galium in particular is highly abundant can be considered relatively high-quality habitat. So, too, can areas—usually the same—where overall food abundance is high. In

TABLE IV. Food Intake by Females in Different Vegetation Zones

Zone	Intake, g/24 h	Intake, g/min of feeding
Nettles	16,602	46.17
Saddle	16,776	45.16
Herbaceous slope	17,439	43.80
Giant lobelia/thistle	17,817	43.88
Brush/ridge	18,387	42.35
Lobelia	18,906	41.05
Afro-alpine	14,067	24.42

such areas, the gorillas satisfied subsistence needs relatively quickly (i.e., foraging time was low). A particularly important role for galium abundance is suggested by the low  $T_{\text{feed}}$  for the saddle zone, where the other variables just mentioned did not reach particularly high values; galium was abundant in this zone and contributed nearly 40% of the diet there [Watts, 1984].

$T_{\text{feed}}$  was lower where food was more clumped (higher index of dispersion), but this relationship may have been due to confounding variables. Partial correlations of  $T_{\text{feed}}$  with the index of dispersion are not significant when either protein biomass, *G. ruwenzoriense* biomass, or stem density is held constant.

Group 4 spent different amounts of time in different vegetation zones (Table I). The intensity with which the group used each zone can be defined as the ratio of the percent of observation time spent within the zone to the percent area of the group's home range that consisted of that zone (Table I). No correlations between activity proportions and either zone use intensity or the absolute number of days per zone were significant. Thus, the gorillas did not concentrate their activities disproportionately in areas where they met subsistence needs most quickly.

### Feeding Time and Food Intake

Table IV gives estimated food intake values for adult females in each of seven vegetation zones. If the afro-alpine zone is ignored, there is a positive relationship between  $T_{\text{feed}}$  per zone and intake per 24 hours, and  $T_{\text{feed}}$  and  $T_{\text{forage}}$  had high inverse correlations with the feeding rate in grams per minute ( $r = -0.97$ ;  $df = 4$ ;  $P < 0.01$  in both cases). Only in comparisons with the afro-alpine zone is the magnitude of differences among zones great for either measure of intake, however. There, the gorillas fed mostly on epithelium stripped from the roots of *Senecio johnstonii* and *Lobelia wollostonii* [Watts, 1984], and both measures of intake were lowest by far. Without the afro-alpine zone, total intake tended to increase as the digestibility of the diet decreased ( $r = -0.79$ ;  $df = 4$ ;  $0.10 > P > 0.05$ ). Addition of the afro-alpine zone, where both digestibility and intake were lowest, confounds this trend.

Unfortunately, data on food energy values are lacking. If it is assumed that energy values vary little among the foliar foods that composed most of the diet (as is the case for foliar foods eaten by western gorillas in Cameroun [Calvert, 1985]), energy intake rates in different zones would probably have had the same ranking as food intake rates. Less energy may have been available from less digestible foods, however, so that there may have been little difference in total energy intake except in the afro-alpine zone.

By feeding preferentially on certain foods that were high in protein content [Watts, 1983], the gorillas maintained a relatively high dietary protein level in most areas other than the afro-alpine zone (Table I). This explains why no

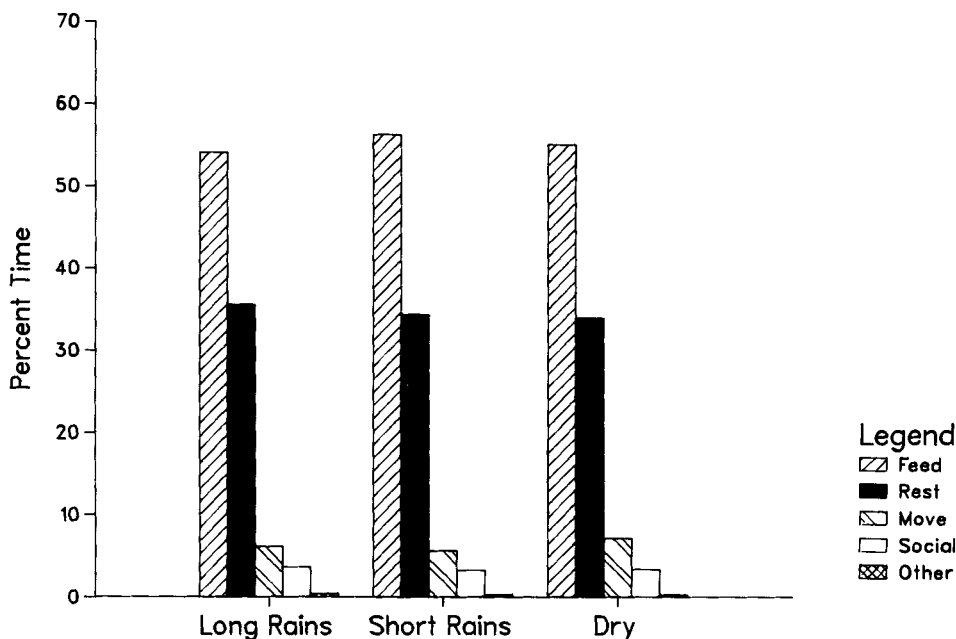


Fig. 1. Amount of time devoted to each activity by Group 4 during each of three seasons.

correlations between dietary protein level and activity proportions were significant (Table III).

### Seasonal Variation

Time spent feeding, resting, and moving by Group 4 and by each/sex class varied little among the dry season (including the inter-rains), long rains, and short rains (Fig. 1). Also, both  $T_{\text{feed}}$  and  $T_{\text{forage}}$  per month varied independently of rainfall for Group 4 (Spearman rank correlations,  $r_s = 0.13$  in the first case;  $r_s = 0.05$  in the second;  $df = 13$ , ns). Coefficients of variation in activity proportions were lower among seasons and among months than among vegetation zones. The gorillas usually interrupted feeding to huddle during prolonged or heavy rain. This inactivity may have had thermoregulatory advantages (a human wearing protective clothing can remain warmer while huddling than while standing upright and moving at the pace of a foraging gorilla), but the animals resumed feeding if rain persisted for more than 2–3 hours. The gorillas apparently made up for any short-term sacrifice of feeding time to huddling by shortening other rest periods and/or by feeding at higher rates after huddling.

### Age/Sex Class Variability

Activity proportions varied little among adult females, blackbacked males, and juveniles. Silverbacks fed longer than all other classes and spent less time moving than did females and blackbacks (Table V). These differences were consistent across vegetation zones (Wilcoxon matched-pairs signed-ranks tests,  $P < 0.01$  in all cases), but were generally small. There were no significant differences among females, blackbacks, and juveniles.

The difference in feeding time between silverbacks and females is small in comparison to the twofold disparity in their body weights. Silverbacks did not



TABLE V. Age/Sex Class Time Budgets in Different Vegetation Zones

Zone	Class			
	Silverbacks	Females	Blackbacks	Juveniles
<b>Feeding</b>				
Nettles	54.1	50.1	49.2	48.2
Saddle	55.0	49.9	52.0	47.8
Herbaceous slope	58.9	54.0	53.9	53.4
Giant lobelia/thistle	60.0	55.1	56.2	54.0
Brush/ridge	64.2	59.4	59.0	58.2
Lobelia	68.7	63.8	61.5	62.1
Afro-alpine	83.4	81.1	79.0	78.3
<b>Moving</b>				
Nettles	4.6	5.9	5.7	6.1
Saddle	5.7	6.8	7.3	7.4
Herbaceous slope	5.4	6.8	6.9	6.6
Giant lobelia/thistle	5.9	7.3	7.2	7.5
Brush/ridge	5.6	6.6	6.7	6.9
Lobelia	6.8	7.5	7.8	8.0
Afro-alpine	7.9	10.1	10.5	10.5
<b>Resting</b>				
Nettles	37.3	42.7	38.8	41.4
Saddle	36.0	36.4	35.0	37.5
Herbaceous slope	35.0	34.9	34.0	32.0
Giant lobelia/thistle	33.0	33.2	32.8	32.9
Brush/ridge	29.5	33.0	32.7	33.1
Lobelia	24.0	28.0	29.2	28.4
Afro-alpine	8.6	8.7	10.3	11.1

ingest food at relatively higher rates: dispersion tests [Cox & Lewis, 1966] on feeding rates for five important foods (Table VI) show no significant variability among age/sex classes ( $X^2 = 0.12$  for *G. ruwenzoriense*, 1.03 for *Carduus nyassanus* leaves, 0.27 for *C. nyassanus* stems, 0.92 for *Laportea alatipes* leaves, and 0.10 for *Peucedanum linderi* stems;  $df = 2$ , ns in all cases). Four sampled females were nonpregnant and nonlactating during some or all of the study; they fed for less time on average (53.2%) when in this condition than when they or other females did when pregnant or lactating (55.8%). The magnitude of the difference was small, but the direction of the difference was consistent across all vegetation zones (Wilcoxon matched-pairs signed-ranks test,  $P < 0.01$ ). This supports the interpretation that the high nutritional demands of reproduction in females account for the small feeding time disparity between males and females. The relatively high  $T_{\text{feed}}$  for juveniles probably reflects the nutritional demands of growth.

Mountain gorilla groups are cohesive, so that the length of foraging paths is similar for all individuals. Silverbacks may have had the lowest  $T_{\text{move}}$  simply because the individuals sampled were less likely than members of other classes to move around for reasons other than to harvest food. There is an indication that silverbacks took slightly more direct foraging paths than did others, however: for each hour of the day, they moved less often between feeding spots per hour than did other classes (Mann-Whitney U-tests,  $P < 0.01$  in each case), but the mean distance covered per move within each vegetation zone did not differ among age/sex classes (Table VII; Kruskal-Wallis test,  $T = 5.2$ ;  $df = 4$ ;  $P > 0.05$ ). The median duration of silverback feeding bouts was longer than that of all other classes in all vegetation

TABLE VI. Age/Sex Class Feeding Rates on Major Foods

Class	No. bouts	Rate	s
<i>Galium ruwenzoriense</i> <sup>a</sup>			
Silverbacks	29	1.69	0.28
Adult females	51	1.65	0.30
Blackbacks	43	1.68	0.42
Juveniles	30	1.70	0.34
<i>Carduus nyassanus</i> leaves <sup>a</sup>			
Silverbacks	51	1.68	0.45
Adult females	23	1.82	0.39
Blackbacks	103	1.68	0.41
Juveniles	28	1.94	0.57
<i>Carduus nyassanus</i> stems <sup>b</sup>			
Silverbacks	26	1.82	0.36
Adult females	20	1.72	0.31
Blackbacks	52	1.91	0.45
Juveniles	22	2.06	0.48
<i>Peucedanum linderi</i> stems <sup>b</sup>			
Silverbacks	25	1.66	0.24
Adult females	20	1.55	0.35
Blackbacks	29	1.70	0.30
Juveniles	23	1.67	0.30
<i>Laportea alatipes</i> leaves <sup>a</sup>			
Silverbacks	27	2.10	0.52
Adult females	27	2.21	0.63
Blackbacks	28	2.19	0.40
Juveniles	19	2.40	0.67

<sup>a</sup>Measured as handfuls per minute [cf. Watts, 1984].

<sup>b</sup>Measured as mouthfuls per minute.

TABLE VII. Median Distance (in m) Moved by Members of Each Age/Sex Class Between Consecutive Feeding Spots in Different Vegetation Zones (No. of Bouts Given in Parentheses)

Vegetation zone	Class			
	Silverbacks	Adult females	Blackbacks	Juveniles
Nettles	3.2 (157)	3.2 (613)	4.1 (456)	2.7 (248)
Saddle	5.2 (254)	4.1 (494)	2.9 (782)	4.2 (223)
Herbaceous slope	4.1 (155)	4.5 (817)	4.2 (1423)	4.1 (1224)
Giant lobelia/thistle	4.1 (103)	4.6 (231)	4.2 (360)	3.8 (257)
Brush/ridge	4.2 (48)	4.7 (197)	4.6 (352)	4.4 (497)
Lobelia	5.1 (60)	5.4 (166)	5.6 (300)	4.9 (159)
Afro-alpine	7.6 (39)	6.9 (196)	7.6 (188)	5.6 (118)

zones (Table VIII; Wilcoxon matched-pairs signed-ranks tests,  $P < 0.01$  in all cases). There were no significant differences among other classes.

### Group Size

Group 4 varied in size during the study and there is some data from other groups; this allows examination of the relationship of feeding time to group size. I have restricted the analysis to data from the herbaceous slope zone, which was the

**TABLE VIII. Median Duration (in min) of Feeding Bouts for Each Age/Sex Class in Different Vegetation Zones**

Vegetation zone	Class			
	Silverbacks	Adult females	Blackbacks	Juveniles
Nettles	5.5	3.1	2.9	3.5
Saddle	6.5	3.4	3.4	3.9
Herbaceous slope	6.5	3.5	3.8	2.3
Giant lobelia/thistle	6.1	3.1	3.1	2.9
Brush/ridge	6.3	3.5	3.8	3.2
Lobelia	5.5	3.2	3.1	2.9
Afro-alpine	7.7	4.7	4.1	3.2

zone used most, in order to control for interzone variation. Data from groups of three or four individuals were combined because sample sizes were small; also, Group 4 had no silverback at these sizes, so the analysis for all group sizes is limited to data on females and blackbacks. The results (Fig. 2) show that there was a positive relationship between feeding time and group size ( $r=0.82$ ;  $df=4$ ;  $P<0.05$ ). Again, however, the magnitude of the differences is very small and less than that associated with variation among vegetation zones.

## DISCUSSION

Mountain gorillas spent most of the day feeding and little of it moving or socializing. Activity proportions varied little seasonally; much more variation occurred in association with nonseasonal differences in food distribution and quality among the different subhabitats (vegetation zones) used by the gorillas. Time spent feeding was directly proportional to group size. Several differences between the activity patterns of males and females were identified, but these were slight, which supports the argument that the ecological cost of permanent association with males is low for females.

### Overall Activity Proportions

Results given here concur with Harcourt & Stewart's [1984] conclusions that gorillas' time spent feeding had earlier been underestimated and with the general positive relationship between feeding time and body weight in primates [Clutton-Brock & Harvey, 1977]. The group feeding time value of 55.4% is close to those reported for orangutans [Rodman, 1977] and chimpanzees [Wrangham, 1977] and higher than those for a number of smaller folivorous primates [colobines: Clutton-Brock, 1974; Struhsaker & Oates, 1975; Marsh, 1981; howlers: Glander, 1975; Milton, 1980; woolly spider monkeys: Milton, 1984]. It is also higher than that given for the same gorilla study population by Harcourt & Stewart [1984]. The discrepancy could be due to their use of point samples (not focal samples) and decision not to consider chewing as "feeding," because of differences in sample time across vegetation zones, and/or because of normal variability among individuals and groups.

As indicated above, food density and abundance varies within a group's home range. In most areas, however, absolute abundance is high and individual food sources, though small, are numerous and densely distributed [Watts, 1983, 1984; Vedder, 1984]. Consequently, the gorillas did not often need to move far between feeding spots or to spend much of the day moving in search of food.

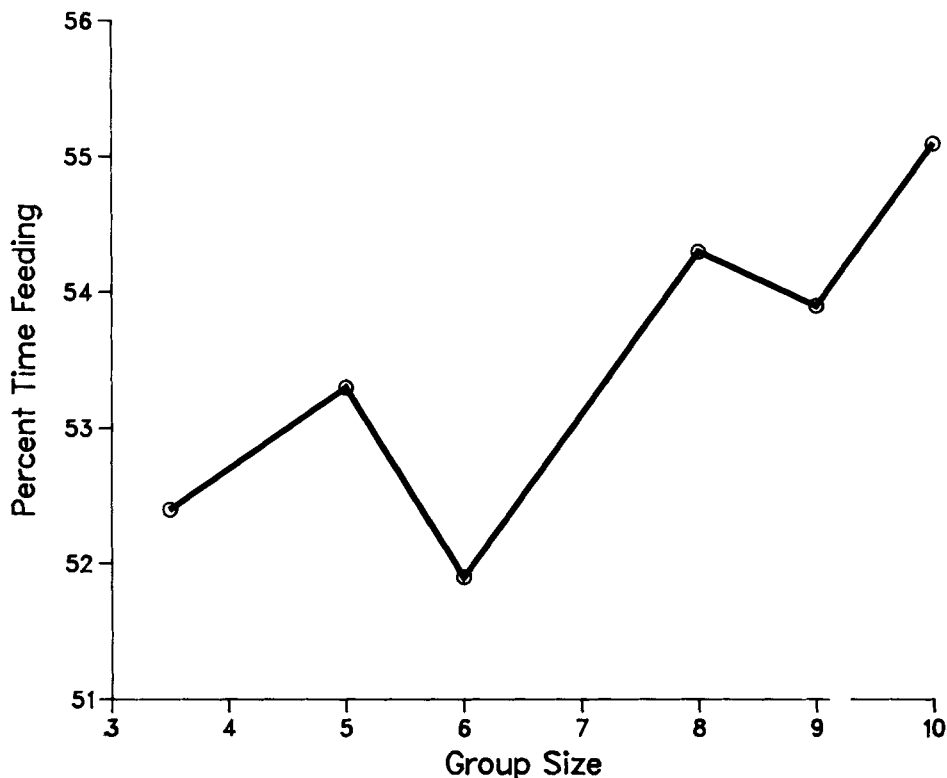


Fig. 2. Time spent feeding by groups of different sizes.

### Seasonal Variability

Most of the gorillas' foods are perennially available, and there was no consistent temporal variability in Group 4's diet [Watts, 1984]. Thus, the time needed to satisfy subsistence needs did not vary among seasons or with respect to rainfall.

### Habitat Variability

Gorilla activity patterns can vary from day to day depending on where the gorillas are within their home range and regardless of season. Members of Group 4 spent less time feeding and moving when in areas where food biomass—particularly *G. ruwenzoriense* biomass—was high; where the density of food sources was relatively high; and where their diet was relatively high in protein and easily digestible. Food protein content and digestibility also influence the food choice patterns of western gorillas [Calvert, 1985], and it might be expected that if there is spatial variation in these factors, it would influence activity patterns in a manner similar to that reported here. This within-habitat variability is analogous, on a smaller scale, to Iwamoto & Dunbar's [1983] finding that the time spent feeding by gelada populations in three different habitats is inversely related to variation in food quality among the habitats.

For herbivores like gorillas, the upper limit to feeding time is presumably set by the relationship of ingestion rate and gut capacity to digestion rate [Parra, 1978]. Outside of the afro-alpine zone, the gorillas probably filled their stomachs

faster than they passed food through the gut, and periods of intensive feeding were followed by prolonged rest. The gorillas fed longer and ate more (except in the afro-alpine zone) when in areas where the average digestibility of their immediate diet was lower. Possibly they compensated for lower digestibility by passing more food through the gut more quickly, as happens in small bodied ruminants [e.g., white-tailed deer; Van Gilder et al., 1982]. They also spent more time moving when in these areas, so that total daily energy expenditure was likely to be higher. It may have been necessary to spend more time feeding to gain the additional energy and/or to compensate for lower energy assimilation rates associated with lower digestibility. In the afro-alpine zone, the gorillas may not have been able to maintain sufficient intake for much longer than their average 6-hour visit.

Saving time by meeting subsistence needs relatively quickly offered two possible advantages. The gorillas rested during most of the additional free time and presumably thereby saved energy. Gorillas are relatively unspecialized herbivores [Chivers & Hladik, 1980], and energy conservation may be important to them, as it is to the ecologically convergent and non-specialized giant panda [Schaller et al., 1985]. Secondly, additional free time would have been available for other activities, such as the development and maintenance of social relationships. Foraging efficiency can constrain time available for social behavior, particularly with regard to maternal nutritional investment in infants [Altmann, 1980, 1983]. Gorillas may not be tightly constrained in this way; they tended to devote little time to socializing even when they spent little more than half the day feeding and moving. They may, however, be constrained by the need for periods of inactivity during which food is digested.

There are several possible reasons why the gorillas did not spend more time in those areas where  $T_{\text{feed}}$  was lowest. They may need to use all zones in order to meet long-term nutritional requirements (including whatever needs are met by epitelium from roots of giant lobelias and giant senecios). Also, they need to allow time for resource renewal after intensive use of a given area; the vegetation takes several months to recover from the effects of gorilla foraging [Watts, 1987], and although not all of an area is disturbed during a single visit, foraging efficiency will diminish if the area is visited repeatedly without allowance for regeneration. Finally, the risk of "predation" affected use of the saddle zone (where  $T_{\text{feed}}$  was low) by Group 4 in 1978–79: the group avoided most of the Visoke-Mikenjo saddle for 5 months after an attack by poachers there in which a silverback was killed. Many of the same individuals, then in different groups, were seen to use saddle areas much more heavily during subsequent periods of fieldwork.

### Group Size

Feeding competition has been implicated as the cause of inverse relationships between feeding time and group size in long-tailed macaques [van Schaik et al., 1983] and yellow baboons [Stacey, 1986]. Baboon and macaque foods tend to be sparsely distributed compared to those of mountain gorillas, and there is interference competition for those that occur in rich, discrete clumps [Dittus, 1977; Post et al., 1980]. In mountain gorillas, there is a direct relationship between supplantation rates at feeding sites and group size [Watts, 1985]; the direct relationship between feeding time and group size reported here suggests an additional cost to social foraging. Supplantations occur at much lower rates than in yellow baboons, however, and the magnitude of the difference in feeding time between the largest and smallest group sizes considered here was slight and was far less than that among vegetation zones. Both of these results suggest that competitive costs are

low, as would be expected given that food sources are numerous and densely and evenly distributed [Terborgh & Janson, 1986]. Data on the time spent feeding by solitary silverbacks, while ambiguous, suggests that sampling error could account for some of the apparent effect of group size: Yamagiwa [1986] gives a figure of 52.7%, lower than that of 60.5% for group silverbacks reported here, but Harcourt & Stewart [1984] give a value of 65% for this same individual.

### Age/Sex Class Variability and Gregariousness

Silverbacks did not feed far longer per day than did females; this is a common finding in mammals in which males are considerably larger than females [e.g., red deer: Clutton-Brock et al., 1982; baboons: Stacey, 1986; Post, 1981; orangutans: Rodman, 1977]. On average, silverbacks had longer feeding bouts than females. This may have been simply because silverbacks have longer arms and can harvest more food at a given spot before having to move [cf. Fossey & Harcourt, 1977]. Females more often extended their arms more than 90 at the shoulder to reach for food and thereby slightly extended their foraging radius [Tuttle & Watts, 1985], but this may not have compensated for the difference in arm length. Silverbacks spent less time moving than did females and blackbacks and may have had shorter foraging paths, but the differences were slight at most. For all age/sex classes, time budgets varied in consistent fashion across vegetation zones.

By associating with males, females can suffer both increased competition for food [Wrangham, 1979] and nutritional costs that stem from problems with the scheduling of activities and/or movement patterns [Rodman, 1979]. Rodman [1985] argues that these disadvantages are too great to allow permanent male/female gregariousness in orangutans, which are highly sexually dimorphic in size and which depend on discrete, localized food clumps available seasonally or irregularly. If males and females stayed together, either males would suffer unsustainably increased energy burdens in trying to keep up with females (who move farther per day), or females, who need a higher quality diet, would make unsustainable nutritional sacrifices by restricting their movements to those of males and thereby encountering a narrower range of foods per day. Wrangham [1979] argues that heavy dependence on scattered, seasonally or irregularly available patches of ripe fruit places limits on chimpanzee gregariousness.

Female mountain gorillas are supplanted at feeding spots more often by silverbacks than by other females [Watts, 1985], but, as noted above, such interactions occur at a low rate. There are no consistent dietary differences between males and females [Watts, 1984]. Both respond to food distribution patterns in a similar manner, and if females traveled farther per day they would tend only to encounter more food sources from the same distribution sampled by males. Low spatiotemporal variability in food distribution helps both to decrease competition and to minimize any advantages to sex differences in activity and movement patterns. Finally, it can be inferred from models of the cost of terrestrial locomotion [Peters, 1983] and transport [Garland, 1983] that costs for females and silverbacks were low, given their low  $T_{\text{move}}$ , and that relative costs were similar for both sexes; thus neither sex makes great energetic sacrifices by restricting movements to those of the other. Permanent association offers males the advantage of increased access to mates. Females benefit from the protection offered by silverbacks against harassment and infanticide by extragroup males [Wrangham, 1979, 1982; Fossey, 1984]; this appears to be more than sufficient compensation for the effects of feeding competition.

## CONCLUSIONS

1. Mountain gorillas spent the majority of their daily activity period feeding. Most of the remainder of the time was devoted to resting, with little time spent moving or socializing.

2. There was no significant seasonal differences in activity proportions.

3. Significant variation in activity proportions was apparent among the different vegetation zones used by the gorillas. This was associated with variation in the abundance, density, and quality of food resources; in particular, the gorillas satisfied subsistence needs more quickly in areas where food abundance and quality were high.

4. Silverbacks spent more time feeding than members of all other age/sex classes and less time moving than did females and blackbacks. Age/sex class differences in time budgets and movement patterns were slight, however; and all classes responded similarly to variation in habitat quality.

5. Time spent feeding was directly proportional to group size, but the effect of group size was small and less than that of differences in food distribution and quality.

6. The results support the argument that the costs of social foraging are low for mountain gorillas.

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