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Time Budget of the Green Monkey, *Cercopithecus sabaeus:* Some Optimal Strategies

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Members of a single group of green monkeys spent, on average, 44.8% of their waking time foraging, 46.7% resting, and 8.5% in social activities, over 1 year. There was significant variation in activity budgets over months (ranging from 35 to 55% of the time spent feeding). Diurnal rhythms of feeding and ranging were influenced by the daily cycle of temperature in predictable ways in different seasons: in the dry season, activity was reduced if it was too hot or too cold, while the temperature in the wet season did not affect activities. Feeding was also synchronized among individuals on a finer time scale, irrespective of the time of day. There was closer synchrony when feeding on less common foods. An ecological model of foraging time and energetics was tested, using estimates of the costs and benefits of foraging and predicting how these are optimally balanced in relation to the food density. Both feeding time and distance traveled increased as food availability increased. Costs and benefits were balanced over several days. Comparisons between populations of Cercopithecus aethiops *were made; differences in time budgets were compared with differences in the availability and quality of food. Insufficient comparative data are available for firm conclusions about the role of different energetic and nutritive strategies in population differences.*

KEY WORDS: *Cercopithecus sabaeus;* time budget; diurnal rhythm; optimal foraging.

INTRODUCTION

The proportions of time that are spent in different activities are important in the ecology of any organism. The variation in activity budgets seen

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in a wide range of species of primates has been shown to suit particular physical characteristics and environmental conditions: for example, the proportion of the day spent feeding is positively related to body weight and negatively related to the proportion of foliage in the diet (Clutton-Brock and Harvey, 1977). Intraspecific comparisions between different populations have also revealed differences in activity budgets (e.g., Kavanagh, 1978; Marsh, 1981; Oates, 1977), but the adaptive significance of these differences remains unclear. Details of food availability are not given, and energetic models of feeding behavior [embodied in optimal foraging theory; see reviews by Krebs and Davies (1978) and Pyke *et al.* (1977)] are rarely considered.

Monthly variation in activity budgets, particularly in the time spent feeding, has been demonstrated within species (e.g., Clutton-Brock, 1974; Homewood, 1978; Kavanagh, 1978; Oates, 1977; Waser, 1977), but although variation in several measures of food availability is implicated, again no conclusive relationship has been stated. It seems that, allowing for differences in body weights and broad dietary characteristics, primates may balance their activity budgets to suit environmental conditions, and precise relationships between these variables should be stated.

There are other ways in which activity budgets vary: many field studies have demonstrated diurnal rhythms of activity (see Clutton-Brock, 1977), but as yet no conclusive statement has been made regarding the functional significance of these rhythms, which may vary over populations of a species or seasonally within a group (Chalmers, 1968; Clutton-Brock, 1974; Struhsaker, 1975; Waser, 1977). The commonly found morning and evening feeding peaks and midday resting period may represent an adaptation to changes of temperature throughout the day, but similar patterns in nocturnal primates (Charles-Dominique, 1971; Doyle, 1974) suggest that digestive factors may also be involved: if feeding is limited by digestion time, early and late feeding peaks may maximize the food intake. Additionally, diurnal variation in the quality of certain foods may affect feeding patterns—for example, fluctuation in the level of alkaloids in plants during the day (Robinson, 1974; Wrangham, 1977).

Social facilitation may act to synchronize feeding and drinking among members of a group (Kummer, 1971). Whatever the mechanism, synchronous feeding and drinking while members of a group are at a feeding site or waterhole may be adaptive in a habitat with widely distributed resources, since an individual leaving the group for food or water at other times might risk being preyed upon.

Five species are recognized within the superspecies *Cercopithecus aethiops* (Dandelot, 1959). An analysis of how one of these, the green monkey, *C. sabaeus,* allotted its time to different activities was carried out, with the following aims:

(i) The first aim was to provide basic data on the activity budgets of green monkeys at Mt. Assirik, in eastern Senegal. The effects of immediate environmental changes (temperature, humidity, rainfall, sunlight) on diurnal rhythms of activity can be examined by looking at the distribution of activities throughout each day. The patterning of resources may influence the degree of synchrony of activities.

(ii) The second goal was to investigate seasonal variation in time budgeting, with reference to variation in available resources. This permits testing models of optimal foraging that involve constraints of time in the balancing of energetic costs and benefits.

(iii) The final objective was to draw comparisons with other populations of the superspécies *C. aethiops,* to investigate adaptive differences in time budgeting that are related to ecological variables.

SITE, METHODS, AND VEGETATION

Details of the study site, climate, vegetation, and sampling methods have been presented elsewhere (Harrison, 1982, 1984). This section is a summary.

The study was carried out from October 1978 to December 1979 at Mt. Assirik (12°53'N, 12°46'W), in the Parc National du Niokolo-Koba, which lies at the border of the Sudan and Guinea savanna zones in southeastern Senegal (see McGrew *et al.,* 1981). The vegetation around Mt. Assirik is a mosaic of woodland (37%), grassland and bamboo (32%), treeless laterite plateau (28%), and narrow strips of gallery forest (3%) (Baldwin, 1979) which grow in steep-sided valleys that cut through the laterite. The core ranging area of the study group of green monkeys was centered on one such valley.

The climate is characterized by two sharply defined seasons: the dry season from November to May and the wet season from June to October (mean annual rainfall, 1976–1979, was 954 mm). There were important microclimatic differences in temperature and humidity among plateau, woodland, and forest: the annual mean difference in temperature between forest and plateau was 9°C, although in the hottest month (April) daily maxima on the plateau averaged 45°C, while maxima in forest averaged only 34°C. The forest also remained more humid than woodland or plateau, throughout the year.

A single study group of monkeys was chosen, in order to record the responses of the same individuals to seasonal variation in climate and vegetation during a complete annual cycle. This group varied in size throughout the year, between 18 and 28 members, depending on births, deaths, and movements of adult males. The group occupied a home range of 1.78 km^2 (Harrison, 1983c). The behavior of individuals in this group was sampled during 5-day, dawn-to-dusk sample periods each month. Details of the activity of each individual in view were systematically recorded using instantaneous scan sampling (Altmann, 1974), at 15-min intervals. Sampling activities at set intervals gives an estimate of the overall amount of the time spent in any given activity. Every 15 min, I scanned the monkeys in view and, for each monkey, dictated a set of data into a cassette tape recorder strapped to my waist. Due to generally poor observational conditions, I allowed a 5-min period, starting at each 15-min interval, in which to walk around and maximize the number of monkeys that was recorded in each scan. To reduce any bias toward eye-catching activities, after spotting a monkey I would pause for a count of five, then record the relevant information. The activity recorded was the "instantaneous activity" (see Marsh, 1981). No monkey was noted more than once in any scan. The following data were recorded for each monkey.

Day: day and month.
Time: time beginning each 15-min interval.
Subject: identity of monkey.
Height: monkey's height above the ground, within 5-m bands—0, on the ground; 5, 0–5 m; 10, 5–10 m, etc.
Activity: one of the following mutually exclusive categories.
  Resting: not feeding or socializing (see below).
  Feeding: foraging, picking, manipulating, chewing.
    Food species (each species was assigned a number, for purposes of computer analysis).
    Food part (bud, flush leaf, flower, fruit, gum, seed, fungus, stem).
    If invertebrate, substrate from which it was collected (leaf litter, earth, foliage, bark, grass).
Socializing:
    Grooming (partners identified under nearest neighbors).
    Playing (partners identified under nearest neighbors).
    Clinging (infants).
Nearest neighbors: identity of any monkey in contact (C) with the subject or within 1 m (N).

Moving was not used as one of the mutually exclusive "activity" categories; in practice it proved difficult to make a quick and clear judgment between moving and resting, since much of the nonforaging movement involved repeated resting stops between movement over short distances. Thus, "resting" was a broad category readily defined as not feeding or socializing. Using range maps to calculate distances traveled provides an unambiguous and independent measure of the energy expended in "moving."

A total of 16,342 records was made in 2090 scans, giving an overall mean of 7.8 records per scan. Most analyses were carried out using SPSS (Statistical Package for the Social Sciences) computer programs (Nie *et al.*, 1975).

To avoid bias toward "visible" activities and, thus, their overrepresentation in scans, the number of monkeys engaged in each activity in each scan was expressed as a proportion of the total number of individuals in the scan. Thus, each record was weighted, with all weightings in each scan adding up to one. So, for example, if feeding was highly visible and resting was not, 10 feeding records in one scan would be equated with 5 resting records in another scan, rather than indicating twice as much time spent in feeding, as suggested by the total numbers of records. The mean percentage differences between the weighted and the unweighted data were negligible (1.2%) and raw, unweighted data were used throughout subsequent analyses.

During each 5-day sample, the location of the group was mapped every 30 min. This involved encircling, on a large-scale map, the area occupied at that moment by the monkeys and noting the time. Thus, from the center of each "circle," distances moved hourly and daily could be calculated. Maps were also divided into 25 × 25-m quadrats, so that various patterns of range use and vegetation could be quantified.

The distribution of important food species in the diet of the green monkeys was recorded in terms of their presence or absence in each of the 2854 quadrats in the monkeys' home range. Important plant species were defined as those constituting at least 5% of any month's diet. The local density of each important species was recorded from a sample of 30 quadrats containing that species. The projected area of tree canopy was sampled from 15 trees of each species and used as a measure of the food-producing area (this assumes a reasonable correlation between crown size and food production). The above sampling was restricted to fruit and flowers. The phenology of important species was also monitored: when fruit or flowers of a species were an important component of a month's diet, the percentage of trees of a species that had fruit or flowers available to the monkeys was quantified from a sample of 50 trees, prior to that month's 5-day sample.

Measures of the overall availability of each food during each month were derived from the above data as follows:

$N \times LD \times m^2 \times AV =$ the total area of tree canopy that contained fruit or flowers available to the monkeys, throughout their range, where N is the number of quadrats containing a species; LD is the local density, trees per quadrat in which that species occurs; m^2 is the mean projected crown area of each tree of that species; AV is the percentage of trees of a species that had food available (from phenological samples).

The total amount of fruit and flowers available each month was calculated by summing the amounts of each important species for that month (see Table V).

RESULTS

Annual Time Budget and Monthly Variation

Of the annual total of 16,342 scan records, 44.8% were of feeding, 46.7% were of resting, and 8.5% were of social activities. An analysis of activities by age and sex class is presented elsewhere (Harrison, 1983b). The proportions of time allotted to different activities varied significantly each month (ANOVA: feeding—$F = 3.35$, $P < 0.002$; resting—see below; socializing—$F = 3.88$, $P < 0.001$) (Fig. 1). Social activities took up relatively little time compared to feeding and resting. There was a high negative correlation between the time spent feeding and the time spent resting ($r = -0.83$, $P < 0.001$), implying that time not devoted to feeding was mostly spent resting, and not necessarily socializing (correlation between time feeding and time socializing: $r = -0.42$, n.s.). An explanation of monthly variation thus needs to be found for only one of these two variables: monthly variation in the time spent feeding is explained within the framework of optimal foraging theory (see below). To anticipate, an increase in the time spent feeding was associated with an increased food availability.

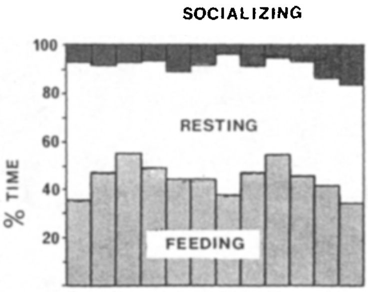

Fig. 1. The proportion of time allotted to feeding, resting, and socializing each month.

Diurnal Rhythms

Feeding

The first hypothesis tested is that feeding activity is broadly related to temperature changes throughout the day. This leads to a prediction about seasonal influences on diurnal feeding rhythms, such that monthly changes in temperature will differentially affect diurnal rhythms. Each hour's four consecutive 15-min scan records were lumped into one record for the hour. Thus, records from 0800, 0815, 0830, and 0845 are combined to form one record for 0800. For each month's 5-day sample, the mean percentages of time spent feeding for each hour of the day were calculated (Fig. 2). Then, for each month, these hourly figures were correlated with the corresponding mean hourly temperatures. The coefficients obtained are shown in Table I.

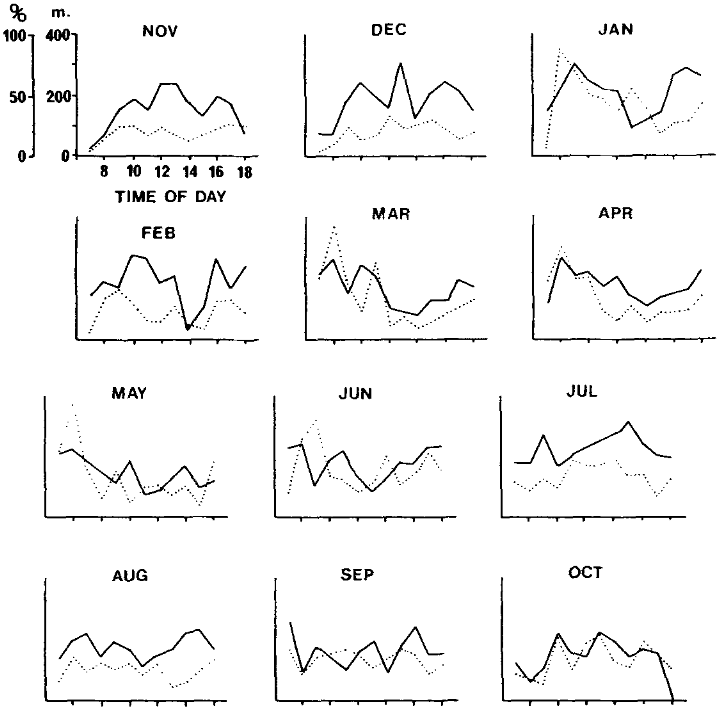

Fig. 2. Diurnal variation in the proportion of time spent feeding (solid line; percentage) and in the distance traveled (dotted line; meters) each hour for each month of the year.

Table I. Coefficients of Correlation Between the Mean Hourly Temperature and the Proportion of Time Spent Feeding and Between the Mean Hourly Temperature and the Distance Traveled Throughout the Day

Month	Hourly temp./% feeding	Hourly temp./ distance
Nov.	$r = 0.70^*$	$r = 0.33$
Dec.	$r = 0.69^*$	$r = 0.72^*$
Jan.	$r = -0.30$	$r = -0.34$
Feb.	$r = -0.07$	$r = -0.10$
Mar.	$r = -0.42$	$r = -0.77^*$
Apr.	$r = -0.46$	$r = -0.84^*$
May	$r = -0.61^*$	$r = -0.55^*$
June	$r = -0.36$	$r = -0.36$
July	$r = 0.52$	$r = 0.30$
Aug.	$r = -0.03$	$r = -0.17$
Sept.	$r = 0.03$	$r = -0.05$
Oct.	$r = 0.49$	$r = 0.56^*$

$^*p < 0.05$.

These coefficients range from high and positive in November to high and negative in May and are correlated with the overall mean monthly temperatures ($r = -0.68$, $P < 0.01$). In other words, in the hottest months the hourly feeding activity was inversely related to the temperature, as the months got cooler the strength of this relationship weakened, and in the coldest months diurnal changes in feeding and temperature became positively related. These relationships are represented schematically in Fig. 3.

However, fluctuations in mean temperature from month to month occurred mainly in the late dry season, from January to May (29.4–34.9°C). During the wet and early dry seasons (June to December), there was little monthly variation in mean temperature (26.4–27.6°C), and yet there was still considerable variation in the above coefficients. Furthermore, examination of each month's diurnal temperature cycle (Fig. 4 gives a sample of 3 months) shows that, although November and December (early dry season) had mean monthly temperatures equivalent to those of the wet season, their cycle of temperatures through the day was different: mornings and evenings were colder than during the wet season, yet midday temperatures were

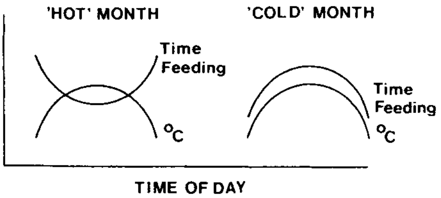

Fig. 3. Schematic diagram to illustrate the relationship between diurnal feeding rhythms and temperature, during a "hot" and a "cold" month (see text).

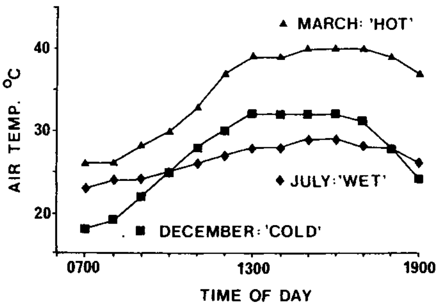

Fig. 4. Comparison of diurnal temperature rhythms among 3 sample months.

higher than during the wet season. Figure 5 shows evaporation and mean temperatures in woodland during each month's 5-day sample: November and December stand out as having "wet-season" mean temperatures, combined with "dry-season" levels of evaporation. This pattern was probably related to the extensive stands of grass remaining after the last rains (October) until the annual grass fires (late December); these stands provided a trap for dew and cool air.

Seasonal influences of temperature on feeding rhythms can thus be divided into three effects.

(i) "Cold" months: early dry season (November and December), before the annual grass fires, when hourly feeding activity and temperature were positively correlated. The monkeys did not feed during the relatively cold mornings and evenings but began to feed as the day warmed up.

(ii) "Hot" months: late dry season, from January to May, when hourly feeding and temperature were inversely related. The monkeys fed primarily in the relative cool of the mornings and evenings and rested during the midafternoon peak in temperature.

(iii) Wet-season months: June to October, when monthly temperatures were all approximately the same, and well within the annual extremes of temperature, and there was no pattern in the relationship between diurnal

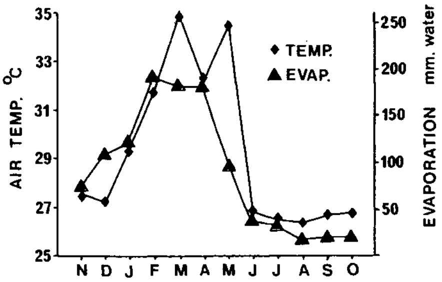

Fig. 5. Mean monthly temperature (C°) and mean daily evaporation (mm of water) during monthly 5-day samples.

feeding and temperature cycles. Thus, temperature had no systematic effect on feeding in the wet season.

Ranging

Patterns of ranging are also likely to be influenced by temperature, rainfall, and humidity. Diurnal variation in the hourly distance traveled is shown for each month in Fig. 2. In an analysis similar to that for feeding rhythms, correlation coefficients for each month were computed for the relationship between the mean hourly distances traveled and the corresponding mean hourly temperatures. The results are shown in Table I. As with feeding rhythms, these coefficients are related to the overall mean monthly temperatures ($r = -0.71$, $P < 0.01$). Distances traveled at each hour during the day were related to temperature changes in the same way as feeding cycles. That is, in the hottest months the hourly distance traveled was inversely related to the temperature, as the months got cooler the temperature exerted less and less influence on traveling, and in the coldest months the hourly distance traveled became positively related to the temperature.

Leaving and Entering Sleeping Sites

The times at which the monkeys leave their sleeping trees in the morning and enter their sleeping trees at night will relate to their daily rhythms of activity. From ranging maps for each 5-day sample, I tabulated, on a daily basis, whether the monkeys left the area of their sleeping site during the first, second, third, etc., half-hour period after dawn and whether they arrived at their next sleeping site in the last, second from last, third from last etc., half-hour period before dusk. Data were analyzed in three seasons—wet, early dry, and late dry—for compatibility with the previous analysis of feeding cycles (Table II).

There were significant seasonal differences in times of leaving and entering sleeping areas [Kruskal-Wallis *ANOVA:* for times of leaving (AM), $H = 11.38$, df $= 2$, $P < 0.01$; for times of arriving (PM), $H = 9.01$, df $= 2$, $P < 0.02$]. Mann-Whitney comparisons of each pair of seasons revealed where the differences lay (see Table II). The green monkeys left the area of their sleeping sites later in the morning during the cold, early dry season than in either the wet or the late dry season ($P < 0.01$), and they entered areas of sleeping sites earlier in the evening during the wet season than during the late dry season ($P < 0.01$). These patterns of leaving and entering sleeping areas were consistent with the seasonal changes in diurnal feeding rhythms.

Table II. Times of Leaving and Entering Sleeping Areas: Frequency (*f*) of Arrival or Departure During *n*th 0.5-hr Period After Dawn or Before Dusk

	Departure (AM)		Arrival (PM)	
	n	*f*	*n*	*f*
Early dry season (Nov.-Dec.)	1	3	1	7
	2	4	2	3
	3	3		
Median	2		1	
Late dry season (Jan.-May)	1	17	1	21
	2	7	2	3
	3	1	3	1
Median	1		1	
Wet season (June-Oct.)	1	21	1	11
	2	4	2	10
			3	4
Median	1		2	

Comparisons. AM: "Early dry" later than "wet," $P < 0.01$
"Early dry" later than "late dry," $P < 0.05$
PM: "Wet" earlier than "late dry," $P < 0.01$

Discussion

Why did the green monkeys respond to seasonal changes in temperature in these ways? During November and December the monkeys rested during the cold early mornings, mostly huddled in small subgroups, and began to feed only when the temperature rose later on. As a method of behavioral thermoregulation, huddling can decrease the rate of heat loss of animals at low environmental temperatures (Kleiber, 1961). The monkeys probably suffered less net energy loss in keeping warm by huddling than by moving around in search of food.

During the hot dry season, from January to May, the daily rhythm of activity was centered around the early-afternoon temperature peak, when the monkeys rested in the relatively cool gallery forest. At this time, the relative humidity in woodland frequently fell below 10-20%, with shade temperatures between 35° and 40°C. On open plateau in the sun, temperatures in the early afternoon often reached 45-50°C. Activity during this period of intense heat could overtax the cooling mechanisms of the monkeys and lead to heat stress: if environmental temperature rises above a critical limit, the metabolic rate no longer decreases and animals cannot get rid of the heat they produce (Kleiber, 1961). The green monkeys almost always headed for the streambed in the valley, to areas of gallery forest with dense cover and water, to drink and rest. On particularly hot days, this rest period lasted up to 3 hr. It was at this time of year that there was the greatest difference in temperature between the streambed (forest) and the area outside the valley (plateau and woodland). The mean difference in hourly temperature between the streambed (forest) and the area outside the valley (plateau and woodland). The mean difference in hourly temperature between woodland and forest was 6°C in the dry season, whereas the mean difference for the wet season was only 1.2°C. Thus the valley provided a relatively cool refuge from the intense "outside" heat, even though temperatures in the valley were frequently 30–35°C on these afternoons.

Thus, in the dry season, the green monkeys' time budget was adjusted so that intensive feeding began at dawn and continued while the relative cool of the morning lasted. Likewise, evening feeding and traveling increased after the inactivity of the afternoon, as the temperatures dropped again. The pattern of very early feeding and ranging was particularly marked toward the end of the dry season, when the monkeys began moving out of their sleeping trees even before dawn and headed for the first feeding sites with barely enough light to see.

The data for February do not fit predictions closely, as is also the case for the selectivity and diversity of the diet (Harrison, 1984). February was probably the hardest month of the year for the monkeys, both climatically and in terms of the low quality and sparseness of food, to which the burdens of pregnancy were added for adult females. However, although the correlations between hourly temperature and feeding ($r = -0.10$) were at odds with the higher negative coefficients for other months in the dry season, the predicted decrease in both feeding and traveling during the afternoon temperature peak was present (see Fig. 2). The low correlations are due to greater fluctuations in the level of activity at other times of day, which were probably related to the lack of predictability of food sources. If food was scarce and poor in quality, the constraints of high temperatures on feeding and ranging may have become relatively less important than searching continuously for unpredictable food.

The third seasonal effect of temperature on diurnal rhythms concerns the wet season, June to October. Correlations showed that the daily cycles of temperature had no simple effect on feeding and ranging during these months. Temperatures in these months were cooler and less variable than during the dry season: wet-season 5-day samples, mean temperatures from 22 to 30°C = 8°C difference; and dry season, from 22 to 40°C = 18°C difference. Early afternoon temperatures of 27–30°C in the wet season would not be enough to overheat an active monkey and, thus, placed no constraints on the activity budget for this period. The main influences on feeding rhythms in the wet season were likely to be, for example, the distribution of food sources, the timing of rainstorms (during which feeding stopped), and the degree of feeding synchrony among individuals.

Feeding Synchrony

The previous section showed predictable effects of temperature on rhythms of activity in certain seasons, i.e., feeding within the group was synchronized broadly with temperature. Here, I examine whether feeding was synchronized among individuals on a finer time scale, irrespective of the time of day. One might expect less need for synchrony when feeding on abundant or evenly distributed foods, whereas at a clumped resource it might be to an individual's advantage to join other monkeys in feeding, despite the cost of increased competition, before the group moved away from that food source. Similarly, a monkey that did not feed with others at a limited resource might risk losing its share.

Two hypotheses are tested: that feeding synchrony occurs irrespective of the time of day and that the degree of synchrony is related to the availability of food.

Methods

Feeding synchrony must be examined within each scan. To what extent are scans made up of all feeding or of all nonfeeding records? For each day during a 5-day sample, each scan that fell on alternate hours was selected. Even hours, from 0800 to 1800, were arbitrarily chosen. Two-hour, rather than one-hour, intervals increase the independence between scans. Three factors were then tabulated: the frequency of feeding vs. nonfeeding monkeys, at six time periods per day, over 5 days. A three-way G test (Sokal and Rohlf, 1969) was applied to each month's data. This test indicates the significance of clustering (synchrony) of the feeding vs. nonfeeding records in each scan, accounting for the time of day and the day of the month. What is being tested is the intrascan dependence, such that a significant result means that frequencies are more clumped (toward feeding or nonfeeding) than expected if the probability of feeding vs. nonfeeding is independent, irrespective of the time of day.

To test for a relationship between the feeding synchrony and the availability of food, a measure of the synchrony associated with each major species of fruit or flowers was calculated. From scan records, the proportion of each scan made up by the various food species was calculated, and for each species, the mean proportion was calculated over all scans in which

Table III. Results of Three-Way G Tests (Activity by Time by Day)

Month	Chi-square value (*G*)	Significance (df = 20)[a]
Nov.	47.8[a]	$P < 0.001$
Dec.	137.2	$P < 0.001$
Jan.	104.8	$P < 0.001$
Feb.	77.5	$P < 0.001$
Mar.	60.4	$P < 0.001$
Apr.	98.8	$P < 0.001$
May	99.3	$P < 0.001$
June	75.0	$P < 0.001$
July	65.4	$P < 0.001$
Aug.	110.4	$P < 0.001$
Sept.	106.0	$P < 0.001$
Oct.	64.2	$P < 0.001$

[a] In November, df = 15: only 4 days' data were used, as 1 day was lost due to tape-recorder malfunction.

it occurred. For example, in December there were 29 scans in which the flowers of *Ceiba pentandra* were recorded, with a mean of 46.1% of the monkeys per scan eating these flowers. Since each scan is taken to be a sample of the activities of all monkeys in the group, this implies that, on average, 46.1% of the group fed on *C. pentandra* flowers whenever these flowers were eaten; in other words, 46.1% were synchronized. Measurement of the overall availability of each food each month has been described above (Site, Methods, and Vegetation).

Results

The outcome of the *G* tests (Table III) shows that in every month there was significant synchrony of feeding among monkeys, which was independent of the time of day and, thus, of the influences of temperature. The strength of the synchrony, as measured by the value of *G*, varied from month to month.

The degree of synchrony associated with each food species is shown in Table IV. This was inversely related to the overall amount of each food available (with *l*n-*l*n transformations, $r = -0.49$, $P < 0.001$): the more food of a particular species there was available throughout the monkeys' range, the less synchrony there was when feeding on that species. (The logarithmic function is explained by the exponential increase in food availability at the higher end of the scale.) This supports the hypothesis that for commonly available foods, there was no advantage to any monkey to synchronize feeding with other monkeys, since there was a high likelihood of these species occurring in other areas that the monkeys visited. On the other hand, for foods with a more restricted availability, a monkey that did not feed when others were feeding was at a disadvantage, since there was less chance of encountering these foods again, in other areas of the range. Further support for this hypothesis comes from a negative correlation between the synchrony associated with a species and the proportion of time spent in quadrats containing that species ($r = -0.28$, $P < 0.05$): the more time that was spent in areas containing a particular species, the less synchronized the monkeys were when feeding on that species. In other words, there was more need for a monkey to feed with others when the group passed through an area quickly, so as not to miss feeding opportunities, whereas if more time was spent there, synchrony was less important.

Further variation in the synchrony associated with various food species was due to several other factors, not quantified here. Species which grew in very open areas, away from dense tree cover, elicited feeding synchrony despite being very abundant. For example, the flowers of *Pterocarpus erinaceus* were common and widely distributed in January but showed a high feeding synchrony. The monkeys often had to cross open ground to reach these trees, many of which were leafless and exposed. The risk to any individual, particularly from aerial predators, would be reduced if many monkeys were feeding in the tree at the same time (Hamilton, 1971), which was frequently the case. There were also species which, particularly at the end of the fruiting cycle, were too few for any synchrony to be possible; for example, the fruits of *Nauclea latifolia* were so rare and dispersed by October that the predicted synchrony was impossible.

In conclusion, there were two factors influencing whether or not the monkeys synchronized their feeding activities: on a broad time scale over each day, changes in temperature determined when peaks of resting and feeding occurred, while on a finer time scale, the degree to which feeding was synchronized was influenced by the availability of each food species.

Optimal Time Budgeting

The green monkeys maintained an optimal diet by adopting certain strategies in their food selection (see Harrison, 1984). For example, they maximized their intake of ready energy by selecting fruit and flowers and ate different species in proportion to their availability; however, as the food density decreased, the diet became more diverse. These strategies concern the contents of the diet and how feeding time should be distributed over various species and food parts. The great spatial and temporal variation in the availability of food over any year also poses a problem concerning the overall energetic costs and benefits of foraging and how to allocate time to various activities. In other words, another strategy concerning the energetics of maintaining an optimal diet should be expected, a strategy governing how time and energy should be spent while in search of patchily distributed foods.

Given the requirements of a nutritive balance in the diet, the monkeys' time budget must allow for a regular intake of invertebrates and small amounts of foliage (Harrison, 1984), but aside from that, the problem becomes one of maximizing the net energy gain after the overall energetic costs and benefits of feeding are balanced out.

The constraints include a certain amount of food available and a certain amount of time in which to feed. The mathematical model discussed by Norberg (1977) and Krebs (1978) predicts that if the density of food is low, the most efficient way to feed is to travel slowly or cover minimal distances (economizing on energetic costs), since this strategy will optimize the net gain under these conditions, even though less time is available for feeding. This may be called a "low-cost, low-yield" strategy. As the food density increases, animals should shift to progressively more costly feeding methods, i.e., traveling fast and far, which is energetically expensive but which allows more time, within the constraints imposed, in which to feed. This can be called a "high-cost, high-yield" strategy.

The data needed to test this model are as follows.

(i) A Measure of the Energetic Cost of Foraging. The day-range length represents the expenditure of energy in searching for food. Implicit in this is a measure of the average speed of movement over a whole day. Monthly mean speeds of movement were calculated, as meters per hour, to account for seasonal differences in the length of daylight (11.5–13 hr). Even with this adjustment, mean speeds of movement correlated highly with day-range length ($r = 0.95$, $P < 0.001$).

(ii) A Measure of the Energetic Benefits of Foraging. I use the amount of time spent feeding on fruit and flowers, the primary choice of food, and the major component of the diet concerned with ready energy [i.e., soluble carbohydrates; see Harrison (1984)]. In terms of the model being tested, the faster an animal travels, the more time there is available for feeding. This measure may have shortcomings for cases where the weight of food ingested is not represented by the amount of time spent feeding on it; however, the discrepancy is most likely to exist between food parts (e.g., fruit as opposed to leaves) rather than within fruits (the main subject of this analysis).

(iii) A Measure of the Food Density. From data on the projected canopy area, local density, number of quadrats containing each species, and

Table IV. Degree of Synchrony (%) Associated with Each Major Food Species Each Month and Number of Scans that Include Each Species (*n*)

	%	*n*
Nov.		
Herbs	40.0	39
F. lecardii	70.1	2
Z. mauritiana	51.7	11
Grasses	29.6	14
Dec.		
C. pentandra	46.1	29
D. mespiliformis	38.2	24
P. erinaceus	50.7	12
Herbs	23.0	25
Jan.		
P. erinaceus	52.2	75
D. mespiliformis	63.0	15
Z. mucronata	75.4	6
D. oliveri	54.4	11
Feb.		
F. umbellata	48.7	25
P. erinaceus	49.8	18
D. mespiliformis	62.1	13
Mar.		
P. microcarpa	47.1	40
L. acida	66.8	15
F. umbellata	41.0	17
Cassia sp.	28.2	21
Ficus sp.	42.0	9
Apr.		
P. microcarpa	46.5	45
S. juglandifolia	44.0	31
F. umbellata	31.1	23
L. acida	49.2	13
May		
S. senegalensis	34.7	41
F. umbellata	30.6	19
L. microcarpa	41.4	35
June		
S. senegalensis	40.3	79
P. lucens	53.2	9
F. umbellata	43.2	13
L. heudelotii	31.9	51
July		
L. heudelotii	52.6	70
F. umbellata	70.4	26
Herbs	30.5	22

Table IV. Continued

	%	*n*
Aug.		
C. lanata	64.3	37
Herbs	27.6	37
Grasses	32.5	29
N. latifolia	35.8	43
A. digitata	40.5	9
S. mombin	49.5	9
Sept.		
S. mombin	52.0	68
N. latifolia	36.0	40
Herbs	25.4	22
Oct.		
Herbs	44.4	54
F. umbellata	67.3	12
N. latifolia	27.2	14
S. mombin	48.4	10
V. madiensis	29.0	16
C. populnea	30.8	11

phenology, for each species there is a measure of the total area of tree canopy with food available to the monkeys. The total for all important species gives a figure for the overall monthly food availability (Table V). Within a fixed home-range area, the total food availability can thus be equated with the food density.

Results

As predicted from the model, the day-range length and the time spent feeding were closely correlated ($r = 0.66$, $P < 0.01$): the faster and farther the monkeys traveled, the more they fed. The model also predicted that these two variables should covary with the density of food, from a low-cost, low-yield strategy at low food densities to a high-cost, high-yield strategy when food was abundant. This prediction is also borne out: day-range length and food density were highly and positively correlated ($r = 0.74$, $P < 0.01$), as were time spent feeding and food density ($r = 0.72$, $P < 0.01$). A logarithmic function may be expected, as there will be an upper limit to the amount of food potential an animal can exploit. As the amount of food continues to increase, the curves for feeding time and travel distance must level off to an asymptote: logarithmic transformation of food densities pro-

Table V. Monthly Values for Time Spent Feeding on Fruit and Flowers (% Time), Daily Distance Traveled (m), and Food Availability (Area in m^2)

Month	% time	Day range	Food availability
Nov.	7.2	952	2,766
Dec.	22.4	943	5,180
Jan.	42.3	2,087	44,844
Feb.	14.9	1,442	4,549
Mar.	29.3	1,640	14,184
Apr.	25.2	1,707	8,418
May	21.0	1,670	12,717
June	28.7	2,020	31,689
July	31.0	1,639	11,028
Aug.	28.2	1,273	7,520
Sept.	29.8	1,639	4,396
Oct.	14.2	1,588	3,238

duced a better linear fit of the data ($r = 0.77$, $P < 0.001$, and $r = 0.79$, $P < 0.001$, respectively; see Figs. 6 and 7).

In conclusion, because of the strong seasonal variation in the density of food that is available at Mt. Assirik throughout the year, the green monkeys adopt a feeding strategy that optimizes the balance of costs and benefits associated with any particular density of food. If food is sparse, they use a "cheap" strategy, economizing on energy expenditure, and as the food density increases, they switch to a gradually more "expensive" strategy, involving increased travel costs but a higher net return on energy from their increased feeding time.

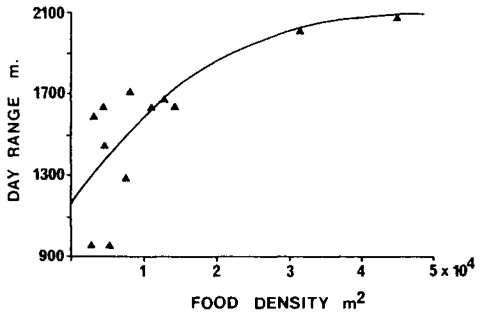

Fig. 6. Mean monthly day-range length (day range; m) plotted against overall monthly food availability (food density; m^2).

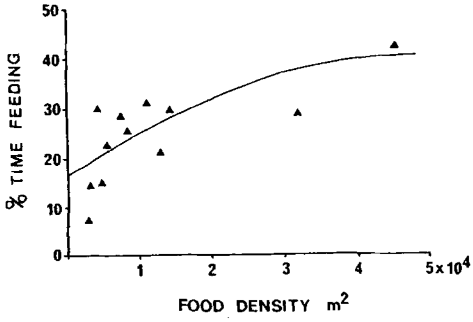

Fig. 7. Percentage of time spent feeding on fruit or flowers (% time feeding) plotted against overall monthly food availability (food density; m^2).

Time Scale

Another question that emerges from the literature on optimal foraging is that of the time scale over which animals are optimizing energy or any other currency (Katz, 1974). For example, foraging behavior that maximizes the net energy obtained by an animal over a week or a month may be different from that which optimizes it over a single day.

In the previous analysis, day-range lengths and time spent feeding were mean figures taken over the monthly 5-day sample periods. There was considerable variation in these measures from day to day. For example, several randomly picked months were examined for correlations between the proportion of time spent feeding each day and the day-range length, and no pattern emerged: January $r = -0.15$, March $r = -0.44$, June $r = -0.12$, and October $r = -0.60$ (all $N = 5$, n.s.). Thus, the very high overall correlations shown in the previous analysis strongly suggest that the monkeys were balancing their foraging costs and benefits over a succession of days. There was no consistent pattern from one day to the next because the monkeys would often feeding on different foods in different parts of their range. One day spent traveling little and feeding intensively in an area of rich fruit supply might be followed by a day of long traveling in search of more widely distributed fruits or monitoring the state of ripeness or availability of new food sources. Nevertheless, these day-to-day feeding and ranging plans still remained within the optimal strategy governing "cheap" or "expensive" foraging, and the energetic costs and benefits were balanced over several days.

DISCUSSION: COMPARISONS WITH OTHER POPULATIONS

Comparing activity budgets across different populations of the same species, in different habitats, can provide important clues to adaptive differences in behavior, but the exercise is fraught with methodological difficulties. Marsh (1981) points out some of the ways in which the measurement of population differences in time budgets is sensitive to the methods used to detect them. He distinguishes particularly between "instantaneous" (i.e., at the instant the target is spotted) and "sustained" (i.e., first activity sustained for 5 sec) scan sampling of activity. Homewood (1978) distinguishes between eating and foraging in her activity records, perhaps a more serious methodological point because the mangabeys (*Cercocebus galeritus*) that she studied spent 35% of their time eating but 49% of the time if foraging was included. A further problem involves equating the feeding time with the rate or weight of food intake (see Hladik, 1977) in different populations.

Studies of *C. aethiops* from which comparative data on time budgets are available include those by Kavanagh (1978), Dunbar and Dunbar (1974), Galat and Galat-Luong (1976, 1977), and Wrangham and Waterman (1981). All four studies specify that they used instantaneous scan sampling. Both Kavanagh and Galat and Galat-Luong included foraging (manipulation, turning debris, etc.) in their feeding records, as in the present study; Dunbar and Dunbar did not (personal communication to Homewood, 1978). Data on the proportion of time spent feeding are available from seven populations (Table VI), although the last two listed are not considered, as they were short studies and the present study indicates much variation in activity budgets throughout a year.

Comparative studies of time budgets have proposed several variables that could account for differences in the time spent feeding: the environmental temperature, since animals require less energy to maintain their body temperature in hotter environments (Marsh, 1981; Oates, 1977), and differences in the diversity of the diet, such that if a monotonous diet is slower to digest than a varied diet, then less time is available for feeding (Marsh, 1981; Struhsaker and Oates, 1975). However, different constraints are likely to apply to colobines and cercopithecines. Inspection of Table VI immediately suggests rejecting both of these hypotheses in the case of *C. aethiops*. The green monkeys at Mt. Assirik showed the highest mean proportion of time spent feeding, and yet Mt. Assirik is among the hottest of these sites. Vervet monkeys at Amboseli also showed long feeding times and yet evinced the lowest diversity of food species.

Many differences in feeding behavior across populations, including time budgets, are more likely to be related to differing floristic compositions of the habitats concerned (e.g., Struhsaker, 1975) and different caloric and nutritive contents of foods at each site (Harrison, 1984; Marsh, 1978). Both Marsh (1981) and Oates (1977), for *Colobus badius* and *Colobus guereza*, respectively, have shown that groups living in poorer, marginal habitats spent less time feeding. This finding concurs with the present study's conclusions about the seasonal variation in feeding time among green monkeys: at times of lower food availability, less time was spent

Table VI. Time Budgets from Seven Populations of *C. aethiops*[a]

Site	%F	(range)	Temp.	*N* sp	Dur.	Author
Mt. A, Senegal	44.8	(35-55)	(30-40)	67	12	This study
Kal, Cameroon	20.0	(17-23)	(30-40)	41	4	Kavanagh
B.N., Cameroon	24.5	(17-36)	(31-40)	26	4	Kavanagh
Amboseli, Kenya	41.0	(21-51)	9-33	9	9	Wrangham
R. Sen., Senegal	–	(23-32)	26-36	17	18	Galat
Saloum, Senegal	8	(70 hr obs. over 7 months)				Galat
Bole, Ethiopia	27.4	(58 hr obs. over 6 months)				Dunbar

[a] %F, percentage of time spent feeding [mean (range)]; temp., mean temperature range [or (seasonal maximal)]; *N* sp, number of food species eaten; dur., duration of study (months).

feeding. This principle may be a strong element in primate feeding strategies, if it is consistent both within and across populations and between species. This study and the two examples given above demonstrate consistency within and between populations. Several other species show a similar pattern of increased activity (ranging and time spent feeding) with increase food availability (e.g., Chivers, 1977; Clutton-Brock, 1975; Raemakers, 1980; Richard, 1977). Notably, baboons consistently show the opposite trend: with decreased food availability, more time is spent feeding (Altmann and Altmann, 1970; Dunbar, 1977; Kummer, 1968; Oliver and Lee, 1978; Sharman, 1981). In addition, vervet monkeys in Kenya also show this trend (Wrangham and Waterman, 1981; see below).

Unfortunately, little attention has been paid to quantifying food availability in many field studies. Only two of the seven sites of *C. aethiops* considered above provide such data: the present study and that by Wrangham and Waterman (1981). It is clear that Amboseli is a relatively simple habitat compared with Mt. Assirik, which has a far greater variety of species and a much higher density of trees (Harrison, 1984). In addition, the green monkeys had a much bigger annual home range than any recorded at Amboseli. These criteria suggest a much higher overall availability of food at Mt. Assirik. However, inconsistent with expectations, from the analysis of optimal foraging (above), the green monkeys did not feed longer than the vervets [Mann–Whitney $U = 34.5$, n.s. (Wrangham, unpublished data)]. A potential problem with this comparison is that no account is taken of the lower overall cost of travel for vervet monkeys around their small ranges in Amboseli. The simple habitat, low diversity of resources, and small home ranges may pose different energetic problems to maximizing the net gain, with different solutions.

Energetics would be unlikely to account for variation between populations in a simple way, since the effect of differences in the nutritive values of foods at various sites may conflict with an energetic strategy. For example, the very low proportion of time spent feeding by the green monkeys in the Sine-Saloum (Galat and Galat-Luong, 1976) in Senegal (8%) is likely to be accounted for by the very high nutritive value of their diet (primarily crabs and mangrove roots). In addition, this rich diet was available with minimal traveling costs, since the food was abundant and densely and evenly distributed. This was a very short study (although not seasonally biased) and probably subject to greater observational bias than most (because of its open beaches and inaccessible mangroves). However, it strongly suggests that food availability is not the only important variable in determining time budgets but that the nature of the diet and its nutritive value may also be an important factor.

Evidence of temperature regulating diurnal cycles in the level of activity is given for several species and study sites, where midday resting peaks are more regular in hotter seasons (e.g., Lindburg, 1977; Kummer, 1968; Richard, 1977). The present study has quantified this relationship in detail, showing that the green monkeys did not feed when it was either too hot or too cold and that in the wet season, the temperature had no effect on activity patterns. These effects were explained in terms of optimal energetic strategies in the face of physiological responses to changes in temperature. Dunbar and Dunbar (1974), Hall and Gartlan (1965), and Kavanagh (1977) all found diurnal variation in the activities of *C. aethiops*. The Dunbars found that feeding increased throughout the day, while the other authors found some tendencies for morning and evening peaks of feeding, but these studies either were short or did not cover all seasons representatively. Clutton-Brock (1974) reported no correlation between temperature and feeding rhythms for red colobus (*Colobus badius*) at Gombe, but there the highest monthly mean temperature was 29°C, only slightly warmer than in the wet season at Mt. Assirik and well below the dry-season temperatures that strongly influenced the green monkeys.

Synchrony of feeding on a fine time scale, irrespective of the time of day (and temperature), has been demonstrated among tantalus monkeys by Kavanagh (1978). He gives descriptive evidence for the significance of this, for example, at clumped trees in open woodland or when termites swarmed for a limited period. Data from Mt. Assirik have quantified this relationship, demonstrating that feeding synchrony became more marked when feeding on rarer foods.

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