

# ACTIVITY PATTERNS OF YELLOW BABOONS (*PAPIO CYNOCEPHALUS*) IN THE AMBOSELI NATIONAL PARK, KENYA

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**Abstract.** Quantitative data on the ways in which adult yellow baboons (*Papio cynocephalus*) distribute their time among various activities are presented. Baboons spend approximately three-quarters of their time feeding or moving. Interseasonal variability in the proportions of time spent feeding and socializing is statistically significant, as are individual differences in the proportions of time spent feeding and moving. Although males and females spend approximately equal proportions of time in each of the activity states, the distributions of the durations of activity bouts show significant intersexual differences in central tendency and dispersion that are consistent with a model of intersexual differences in overall foraging strategies. Consistent diurnal patterns are conspicuously absent, and the relationship between this finding and other ecological variables is discussed.

As Struhsaker & Leland (1979, page 162) have noted, 'an analysis of how different species distribute their time among various activities is essential to any characterization of their life styles, and lays a foundation for interrelating their ecology and behavior'. Interspecific variability in activity budgets among primate species is quite marked, and recent work has suggested that some of this variability, at least, may be attributable to body size and dietary variability within the Order (Clutton-Brock & Harvey 1977, page 365 ff.). Specifically, the proportion of foliage in the diet is negatively correlated with the proportions of time spent feeding and moving and positively correlated with the proportion of time spent inactive, while body size is positively correlated with feeding time once the dietary variable has been factored out (Clutton-Brock & Harvey 1977; Gaulin 1979; Struhsaker & Leland 1979). General constraints of this nature may lie behind the distinctiveness of the activity profiles of different species (Bernstein 1976; Davis et al. 1968), although intraspecific variability in activity budgets has been documented in many species and may reflect fluctuations in resource availability or other environmental variables (Clutton-Brock 1977).

Although both the ecology and the social organization of baboons have received considerable attention, little quantitative information is available concerning the ways individual ba-

boons distribute their time among different activities. This report presents data gathered during systematic focal-animal sampling of adults within a single social group of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park in Kenya during the period from October 1974 to August 1975. These data are examined for interseasonal, interindividual, and diurnal variability in the amounts of time spent in each of four activity states (feeding, moving, resting, and socializing); however, as this report forms part of a larger study primarily concerned with feeding and ranging patterns in this group (Post 1978), feeding and moving will be most closely scrutinized. The flexibility of the baboons' behavioural responses to fluctuations in resource availability has frequently been cited as an essential component of the adaptive strategy that has resulted in the successful colonization of most of Africa (Rowell 1966; Altmann & Altmann 1970; Nagel 1973; Altmann 1974). Thus the analysis of the nature and causes of variability in activity proportions can contribute to our understanding of the nature of that adaptive strategy.

In addition, the focal-animal sampling technique employed allows for the examination of the distributions of feeding and moving bout durations. My interest is primarily in the information these distributions provide concerning interindividual, and particularly intersexual, differences in foraging habits beyond that provided by the the analysis of activity proportions

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alone. The assumption that these distributions reflect both the characteristics of the distribution of food resources and the extent of inter-individual competition for food is not explicitly addressed in what follows (see Slatkin 1975; Post et al. 1980). Given that individuals within a single foraging group face similar distributions of available food, at least insofar as they feed on the same range of foods in the same areas (see below), these bout duration distributions may reflect the extent to which individuals are affected by, and the manner in which they respond to, that competition for food (see Discussion).

### Methods

A detailed account of the structure and dynamics of the Amboseli ecosystem can be found in Western (1972), and a description of the ecology of baboons and vervet monkeys (*Cercopithecus aethiops*), along with general ecological characteristics of the area, can be found in Altmann & Altmann (1970) and Struhsaker (1967). Briefly, the habitat frequented by baboons within the Park can be characterized as semi-arid short-grass savanna. The area is dominated by grasses of the genus *Cynodon* (e.g. *C. dactylon* and *C. plectostachyus*) and *Sporobolus* (e.g. *S. kentrophyllus*, *S. marginatus*, and *S. africanus*). Rainwater from neighbouring Mount Kilimanjaro percolates into the Amboseli Basin and surfaces as swamps and permanent waterholes. Water is also available in small rainpools during the rainy season months (see below). Permanent waterholes and other depressions are surrounded by relatively dense groves of yellow-barked fever trees (*Acacia xanthophloea*) and a dense understory dominated by the shrubs *Azima tetracantha* and *Salvadora persica*. In drier regions, the umbrella tree (*Acacia tortilis*) is dominant.

Data on rainfall and temperature, collected at a small weather station established at our camp approximately 12 km from the border of the study group's home range, are summarized in Fig. 1. Seasonal temperature variability is slight, while rainfall variability is quite marked; most rain falls during the long rains (March–May) and the short rains (November–January), and the intervening dry periods will be referred to as the inter-rains (February) and the dry season (June–October) (Altmann & Altmann 1970).

Observations were made of members of Alto's group (see J. Altmann et al. 1977), which numbered 46 individuals at the start of preliminary

data collection (July 1974) and 50 individuals at the termination of the study (August 1975). Data on changes in group composition due to births, deaths, immigrations, and emigrations are presented elsewhere (Post 1978, Table 1).

Data presented below come from focal-animal samples (see J. Altmann 1974) on a subset of adults in Alto's group. Four adults (two males and two females) were initially chosen at random from among the 25 adults in the group; a fifth individual, adult male Chip, was added to this subset as a 'back-up' in case one of the males emigrated or died, although sampling of Chip's behaviour was somewhat less systematic than sampling for the behaviour of the other four focal animals (see below).

Each focal animal was followed for an entire day (0700 hours to 1800 hours) at a time. I chose each day's focal animal in such a way that each of the four main focal individuals was observed for two days during the first eight sample days of every month. Chip was the focal animal during the following day. During any remaining sample days in a given month focal animals were chosen at random from the set of five individuals.

Sampling proceeded as follows (see Post 1978 for a more complete description of sampling methods): the focal animal was observed continuously during 15-min samples beginning on the half-hour (0730 hours to 1730 hours), during which the following information was recorded: the activity state occupied (see below for a definition of these states), transition times between activity states, and all foods eaten during feeding bouts. Total sample time on each of the

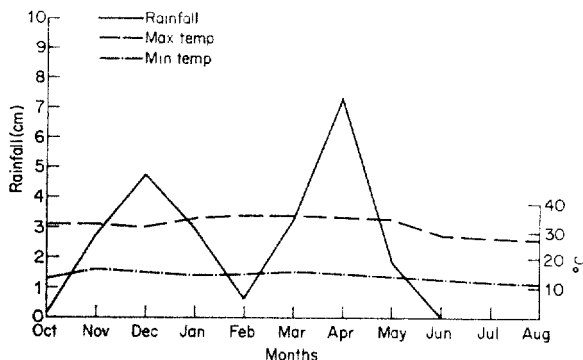


Fig. 1. Mean monthly rainfall (cm) and mean monthly maximum and minimum temperatures during the 11 study months.

five focal animals during each of the 11 months of the study is given in Table I.

Due to the difficulty of maintaining my concentration during 11 daily samples of this kind, one major modification of the procedure described above was introduced: the samples at 0730 hours and at three other times chosen at random were 'feeding only' samples, which were identical to those described above except that only feeding bouts were recorded.

I defined activity states to make the list of such states both exclusive and exhaustive, so that an animal could occupy only one activity state at any time. Five activity states were defined as follows:

**1. Feeding.** Feeding began when the subject first made contact with any part of a food plant, excluding contact with the plant as a locomotor substrate. Feeding bouts terminated when the subject either (a) moved more than one full stride, even if it was carrying part of the plant in its hand or mouth, or (b) stopped looking at the food plant. By this definition, a switch to a new food type in the absence of either of these conditions was not sufficient for the bout to be considered terminated; thus a single feeding bout could include more than one food type.

**2. Moving.** This category included all locomotor activities, e.g. walking, running, climbing, and leaping between arboreal supports, but excluded short movements during feeding (less than one full stride) and locomotion during social behaviour (e.g. the subject chased another individual).

**3. Resting.** This category included solitary behaviour during which an animal was neither feeding nor engaged in social behaviour, and included sleeping, auto-grooming, looking about, etc.

**4. Social behaviour.** Social behaviour included all periods of activity during which an animal's

attention and behaviour were clearly directed toward another individual. This category included allo-grooming, mounting, perineal presentation, chasing, play, aggression, etc.

**5. Drinking:** Drinking included all times during which an animal's mouth was in contact with water. Because animals spent so little time drinking, drinking will not be analysed below.

## Results

### Proportions of Time Spent in Different Activities

Estimates of the proportions of time spent in the different activity states are displayed by month in Table II and by season in Table III. Each monthly estimate was computed by:

(a) calculating from the focal-sample data the proportion of time spent in each activity state during each hour of each day that month;

(b) taking the mean of these 11 hourly estimates as the estimate of the proportion of time spent in each activity during the day in question; and

(c) calculating the mean and SD of these daily estimates for all days in the month in question.

This procedure corrects for the potential bias due to the unequal distribution of observation time among different hours in a manner analogous to the method used in Altmann & Altmann (1970, pages 120-121). The seasonal estimates in Table III are the means of the estimates for all months within each of the four seasons.

Finally, these monthly proportions were averaged to calculate an overall mean proportion of time spent in each activity (Table II, 'Mean'). Overall, the baboons spent close to half of the time between 0700 hours and 1800 hours feeding, and approximately 70% of that time either feeding or moving. The standard deviations in Table II reflect day-to-day variability within months in the proportion of time spent in different activities, and it is clear that this variability is large for almost all months and

Table I. Sample Times

A. Focal-animal sample (min)		Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Total
	Animal												
Male	Stubby	98	184	135	349	265	234	322	291	431	337	146	2792
Female	Brush	126	214	202	183	393	264	348	308	328	451	250	3060
Male	Peter	66	246	126	243	250	175	249	190	241	274	231	2291
Female	Preg	136	173	117	372	269	423	273	292	346	395	169	2965
Male	Chip	0	0	0	142	126	271	91	154	128	207	0	1119

activities. Averaging the monthly coefficients of variation (CV) for each of the four activity states yields mean CV's of 19.90 (feeding), 33.47 (moving), 47.04 (resting), and 83.09 (social behaviour). Some of this variability may be due to interindividual differences in activity proportions, discussed below.

The significance of interseasonal and inter-individual variability in activity proportions was tested with a two-way analysis of variance with replication (Sokal & Rohlf 1969, page 299). The proportion of time spent in each activity each day (using the arcsin transformation for proportions, Snedecor & Cochran 1967, page 327) was the dependent variable, with season and focal-animal identity as the 'treatments'. Inter-seasonal differences, adjusted for differences among the five focal animals, are significant for feeding ( $F = 4.51$ ,  $df = 3,80$ ,  $P < 0.01$ ) and social behaviour ( $F = 3.41$ ,  $df = 3,80$ ,  $P < 0.05$ ). Interseasonal variability in moving and resting proportions is not significant. The proportion of time spent feeding is highest and the proportion of time spent socializing is lowest during the long rains and the dry season, and the opposite is true during the short rains and inter-rains (Table III). The proportions of time spent

feeding and socializing each month are strongly negatively correlated (Table II;  $r_s = -0.884$ ,  $N = 11$ ,  $P < 0.01$ ). However, these proportions are not strictly independent since the sum of all four proportions each month must equal unity, and therefore the significance of this correlation is difficult to assess (see Discussion).

Interindividual differences, adjusted for seasonal variability, are significant for feeding ( $F = 3.14$ ,  $df = 4,80$ ,  $P < 0.05$ ) and resting ( $F = 2.81$ ,  $df = 4,80$ ,  $P < 0.05$ ) and are close to statistical significance for moving ( $F = 2.44$ ,  $df = 4,80$ ,  $P \sim 0.10$ ). The small number of animals sampled prevents attributing this variability to effects of age, dominance rank, reproductive condition, or other variables that may be causally linked to the proportions of time animals spend in different activity states. The two females spent a significantly greater proportion of time feeding during days on which they were pregnant or lactating (Mann-Whitney  $U$  test, one-tailed,  $P < 0.05$ ). However, the reproductive conditions of the females were roughly synchronized during this study (see Table VII in Post (1978)), both having conceived in early 1975 (9/1/75 for Preg and 17/2/75 for Brush, assuming six-month gestation). Thus this differ-

Table II. Proportion of Time Spent in Each Activity

Month	% Feeding	SD	% Moving	SD	% Resting	SD	% Socializing	SD
Jan.	35.22	9.14	28.90	11.74	23.04	8.40	11.61	9.24
Feb.	43.93	8.81	20.86	4.85	24.03	10.27	9.82	8.10
Mar.	45.81	12.60	24.99	8.73	23.18	14.41	5.64	6.91
April	51.36	9.05	20.43	7.92	19.19	7.58	6.11	6.07
May	53.23	9.41	23.64	6.83	21.17	9.29	5.55	5.56
June	53.58	9.14	24.74	5.66	16.79	10.56	5.45	5.02
July	54.98	9.19	22.77	8.96	17.48	6.78	3.70	3.40
Aug.	43.09	15.53	17.40	5.85	31.01	17.21	7.45	5.23
Oct.	44.11	3.51	24.25	11.43	22.56	6.93	8.39	2.10
Nov.	47.70	9.97	27.07	6.41	19.73	11.34	4.80	5.34
Dec.	37.85	4.34	27.55	9.65	21.49	10.20	12.72	4.93
Mean	46.44	6.47	23.87	3.39	21.79	3.86	7.38	2.92

Table III. Seasonal Distribution of Activity Percentages

Season	% Feeding	SD	% Moving	SD	% Resting	SD	% Socializing	SD
Short Rains	39.84	9.75	27.99	9.46	21.62	9.52	9.70	7.85
Inter-Rains	43.93	8.81	20.86	4.95	24.03	10.27	9.82	8.10
Long Rains	50.07	10.57	22.91	7.88	21.11	10.53	5.79	6.01
Dry	51.08	9.96	22.57	7.97	20.35	11.34	5.48	4.38

ence in feeding time cannot be definitely attributed to this change in reproductive condition but may be due to a seasonal effect or to some interaction between the two. Figure 2 shows the mean activity proportions for the three males and two females (monthly and seasonal breakdowns of these proportions can be found in Post (1978)). The differences in activity proportions between males and females in Fig. 2 are not significant (Mann-Whitney *U*-test, two-tailed, using the 11 monthly means for each of the four main focal animals). This accords well with the results from an earlier study (Post et al. 1980) with a larger sample of animals, in which there was no significant difference between males and females in time spent feeding.

No significant correlations (Spearman rank correlation) were found between the average monthly proportion of time spent in any activity state and (a) monthly rainfall, (b) previous month's rainfall, (c) sum of (a) and (b), (d) mean temperature at 1430 hours, or (e) mean daily maximum temperature. In contrast, J. Altmann (1980) has recently reported that in a later study on adult female activity budgets in Alto's groups the sum of the rainfall in one month plus that of the previous month accounted for a significant proportion (50%) of the variance in average monthly time spent feeding.

### Diurnal Distribution of Activities

The mean time spent in each of the four major activity states during each hour for each of the four seasons is shown in Fig. 3; the diurnal distribution for the entire 11-month period is given in Fig. 4. The values shown in these figures are the means of the daily estimates for each

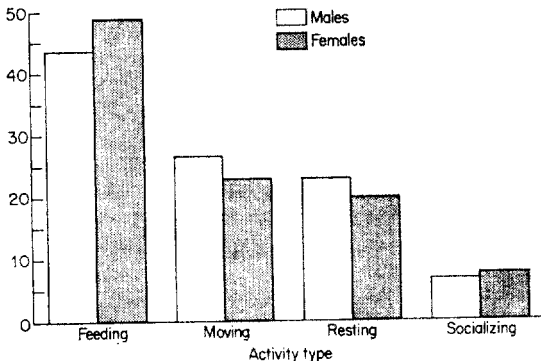


Fig. 2. Mean proportion of time spent in the four activity states by the three males and two females.

hour for each of the activities. Daily variability in all hours and all activities is high; over the entire sample, the mean hourly coefficients of variation are 58.7, 79.5, 123.0, and 267.1 for feeding, moving, resting, and social behaviour, respectively.

In three of the four seasons the diurnal pattern of feeding behaviour approximates a triphasic pattern, with early morning, midday, and mid-to-late-afternoon feeding peaks (Fig. 3). The timing of these peaks, in terms of actual 'clock time', varies from season to season, with the result that the pattern for the entire study (Fig. 4) shows no evidence of feeding peaks but rather a steady rise throughout the day in the proportion of time devoted to feeding. The dry season pattern, too, shows a steady increase in time spent feeding and a concomitant decrease in the proportion of time spent moving and resting (Fig. 3).

The significance of the diurnal variability depicted in Figs 3 and 4 in time spent in the four activity states was tested by means of the following variant of the median test. For each day the proportion of time spent in each of these four activity states during each hour was calculated, and the median proportion of time spent in each activity state for that day was determined. For each hour I then recorded whether the proportion of time spent in an activity was greater or less than the median proportion of time spent in that activity that day. This procedure was repeated for all days within each of the four seasons, and the entire process was then repeated for the other three activity states. The hypothesis to be tested is that the proportion of time spent in a given activity state during a given hour is equally likely to be above or below that day's median proportion of time in that activity state; that is, the observed number of times the activity proportions for a given hour fell above and below the median was compared to the cumulative binomial distribution with  $P = 0.5$  and  $N =$  number of days for which data from that hour are available.

The results of this analysis, using data for all seasons pooled together, are shown in Table IV; entries for each hour show the number of days during which the proportion of time spent in each activity state fell above and below the daily median proportion for that activity, and the probability, under the null hypothesis of a 1:1 ratio, of obtaining a deviation as large as that observed. The results are striking in that there appears to be virtually no tendency for the animals to 'prefer' certain hours for any of the

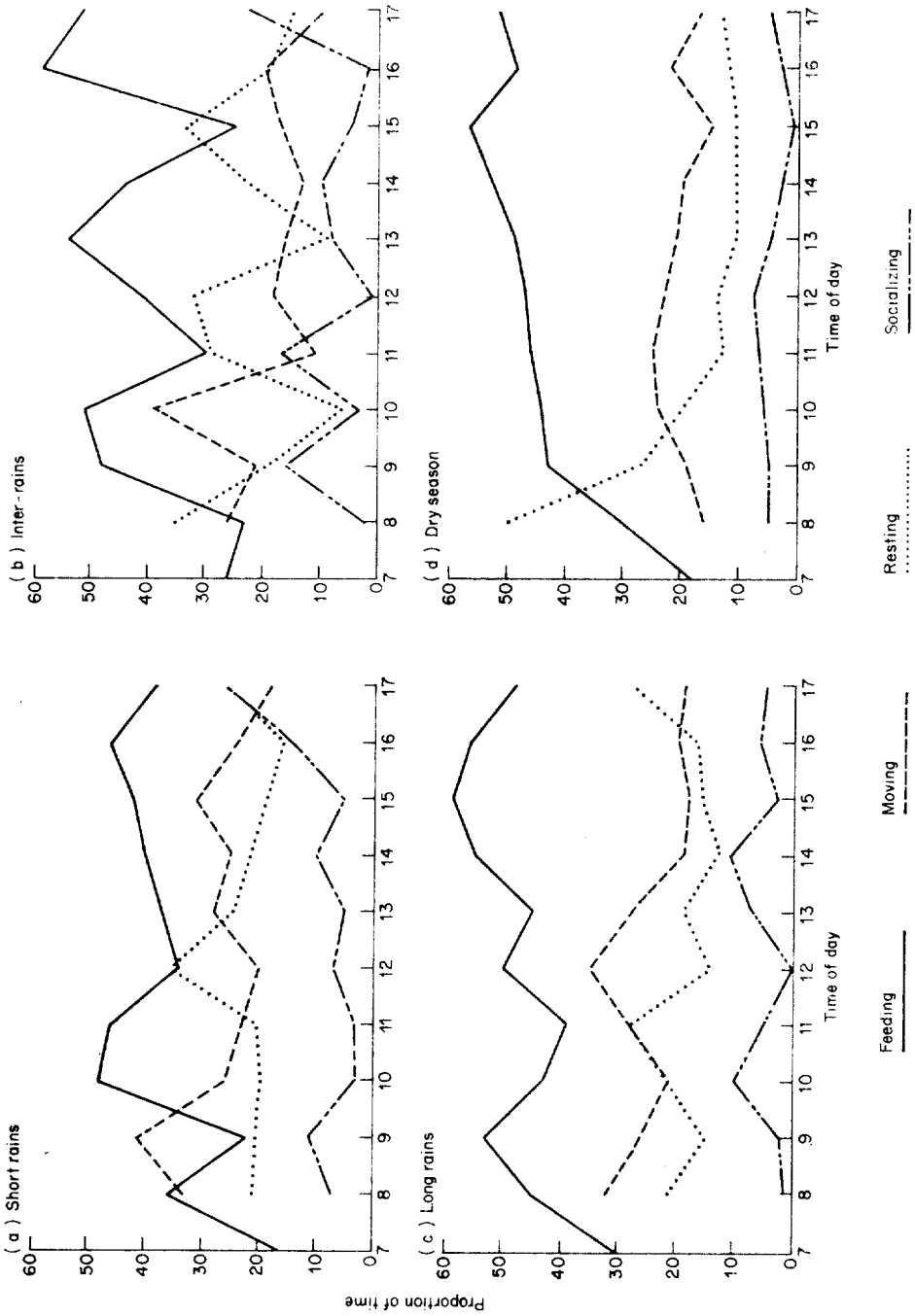


Fig. 3. Diurnal distribution of activity proportions during each of the four seasons.

activities over the course of the year; only 3 of the 41 observed distributions (feeding, 0700 hours and social behaviour, 0900 hours and 1500 hours) deviate significantly from the expected ratio. This is approximately the number of falsely rejected null hypotheses (Type I errors) expected when working at a significance level of 0.05, and thus the overall picture is very different one of independence between time of day and intense periods engaged in any one activity. With the exception of the first hour, for which only feeding data are available (see Methods), only the hour beginning at 1500 hours shows a reasonably consistent overall activity pattern, with a tendency towards high feeding scores and low scores for the other three activities (Table IV).

This test was repeated using data from each season considered separately (not shown), and a similar absence of a pattern emerged: in only 7 of the 164 cases (41 cases in each of four seasons) could the null hypothesis be rejected.

I examined these data for evidence of inter-seasonal or intermonthly variability in the amount of time spent in each of the four activity states during each hour. Data from the 11 months were grouped into seasons, and sample estimates of the proportion of time spent in each of the four activities during each hour were compared among the four seasons by means of the Kruskal-Wallis test (Siegel 1956), with the null hypothesis that the mean is the same in all four seasons. The null hypothesis could be rejected in only 8 of the 41 comparisons; the hours showing significant interseasonal variability have been marked with an asterisk in Fig. 4 (the nature of the interseasonal variability in the activity pattern during these hours can be as-

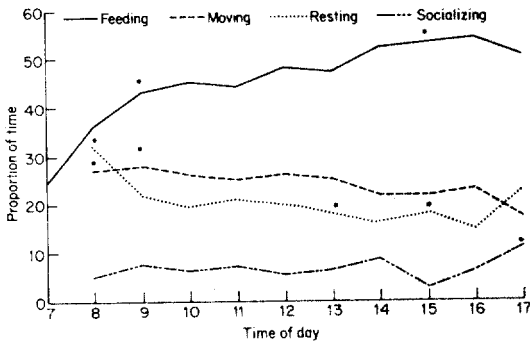


Fig. 4. Diurnal distribution of activity proportions averaged over the entire study. An asterisk denotes those hours and activities that showed significant interseasonal variability. See text for details.

essed with reference to Fig. 3). These results do not lend themselves to simple interpretation: non-significant results are as often due to high within-season variability as to interseasonal equality of the means. With one exception (resting, 1300 hours) all significant differences occur during the first three (0700–1000 hours) or last three (1500–1800 hours) hours. The general pattern appears to be a steady increase in the time spent feeding during the first three hours (exception: short rains, 0900 hours), with moderate amounts of time moving (exceptions: dry season, 0800 hours (low) and short rains, 0900 hours (high)) and resting (exception: dry season, 0800 hours). There is a resting 'peak' and feeding 'valley' at 1500 hours during the inter-rains. Early morning and late afternoon peaks in social behaviour (Altmann & Altmann 1970, page 93) were apparent only during the short rains and inter-rains.

Finally, I attempted to assess the effect of feeding during any given hour on the proportion of time spent feeding during the subsequent hour. Matrices whose  $(i, j)$ th entry represented the number of days during which the focal animal fed for  $i\%$  of the time during hour  $x$  and  $j\%$  of the time during hour  $x + 1$  were drawn up. For computation purposes, the proportion of time spent feeding was divided into 10 intervals (0–9.9%, 10–19.9% . . . , 90–100%). Five  $10 \times 10$  matrices were drawn up, one for each of the four seasons and one for the pooled data for all 11 months (Post 1978, Tables 12–16). The null hypothesis that the proportion of time spent feeding during hours  $x$  and  $x + 1$  are independent was tested by means of the  $G$ -statistic (Sokal & Rohlf 1969, p. 599). Only during the dry season does the null hypothesis of independence fail to fit the observed data, with the suggestion during that period of a tendency for high feeding proportions during one hour to be more frequently followed by high feeding proportions in the subsequent hour than would be expected under the null hypothesis (Post 1978, pages 29–31).

In sum, there is little evidence either that certain activities are performed at higher-than-expected frequency during any hour (with the possible exception of a feeding 'valley' at 0700 hours and a feeding 'peak' at 1500 hours) or that predictable hour-to-hour patterns exist, irrespective of 'clock time', in the proportion of time spent feeding. Although the within-season diurnal activity distributions (Fig. 3) appear to show more distinct patterns, the within-season

Table IV. Analysis of Activity Peaks (See Text)

Time of day (hours)	Feeding			Moving			Resting			Social behaviour		
	Number of times			Number of times			Number of times			Number of times		
	Above median	Below median	<i>P</i>	Above median	Below median	<i>P</i>	Above median	Below median	<i>P</i>	Above median	Below median	<i>P</i>
0700-0800	11	34	0.001	32	27	0.603	35	25	0.245	31	28	0.795
0800-0900	32	49	0.075	39	28	0.222	34	31	0.804	27	32	0.603
0900-1000	37	46	0.380	37	32	0.630	32	34	0.902	23	40	0.043
1000-1100	42	43	1.000	29	29	1.000	35	25	0.245	25	30	0.590
1100-1200	35	42	0.494	29	13	0.851	14	13	1.000	10	17	0.248
1200-1300	22	23	1.000	15	29	0.532	37	27	0.260	27	33	0.519
1300-1400	40	43	0.826	35	29	0.905	29	40	0.228	34	35	1.000
1400-1500	49	37	0.235	34	36	0.064	30	39	0.335	21	44	0.006
1500-1600	51	36	0.133	29	46	0.064	30	39	0.335	21	44	0.006
1600-1700	49	34	0.124	35	29	0.532	25	39	0.103	34	31	0.804
1700-1800	40	28	0.182	21	32	0.167	26	25	1.000	20	29	0.253



picture is likewise one of independence between the hours of the day and the animals' activity. Although the timing of periods of intensive activity differs interseasonally, in the absence of a coherent interpretive framework the overall significance of this variability is obscure.

#### Duration of Activity Bouts: Interindividual Differences

As shown in a previous section, the gross activity profiles of adult males and females tend to be similar, with a suggestion of a non-significant difference whereby males spend somewhat less time feeding, and somewhat more time resting and moving, than females. However, the way in which males and females partition their total time within any activity state into individual activity bouts seems to differ substantially, and this difference may reflect important differences in their utilization of environmental resources. An activity bout was defined as an uninterrupted period within one activity state. Figure 5 shows the mean length of feeding and moving bouts

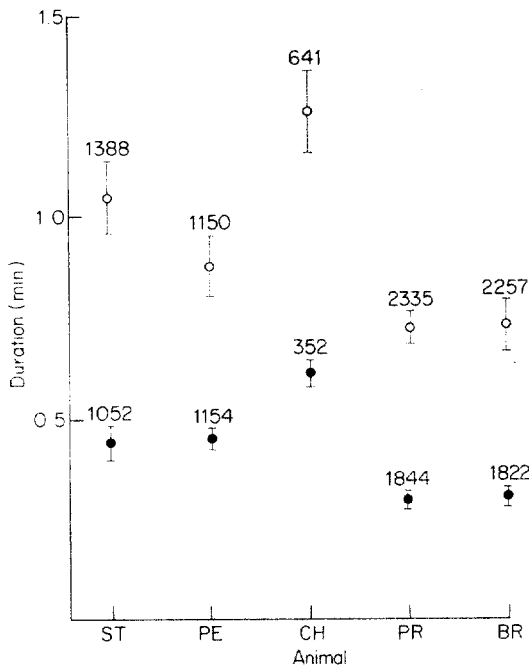


Fig. 5. Mean feeding (open circles) and moving (closed circles) bout durations for the five focal animals. ST = Stubby (male), PE = Peter (male), CH = Chip (male), PR = Preg (female), BR = Brush (female). Vertical bars represent two standard errors, and numbers above the vertical bars represent the number of bouts observed for that animal.

for the five focal animals, and it is clear that males have longer average feeding and moving bouts than females (all pairwise male/female comparisons are significant by *t*-tests). Mean bout durations were computed using the technique of Kaplan & Meier (1958) to correct for the bias introduced by the use of 'censored' bouts (i.e. bouts without a known starting or termination time due to the subject moving out of sight behind a bush, beginning and ends of samples, etc.). Note that the larger number of female bouts (Fig. 5) is consistent with the roughly equal amounts of time that males and females spend feeding and moving (Fig. 2) and the longer mean bout durations of the males.

Several factors may account for the longer feeding bouts of males. First, the diets of males and females differ significantly (Post 1978, and in preparation), and the 'average' female diet may consist of a smaller proportion of foods distributed in large 'patches' capable of supporting long feeding bouts. A second set of factors would apply even if males and females included identical proportions of the same foods in their diets. For example, males may feed more slowly than females, thus spending more time at a food site to ingest the same quantity of food. This is unlikely to account for the observed difference in mean feeding bout duration since there does not appear to be a consistent tendency for females to feed at faster (or slower) rates than males (Post 1978; Rhine & Westlund 1978; Post et al. 1980). Males may exploit feeding sites with larger quantities of food, or males and females may utilize different criteria for the termination of feeding bouts such that males extract a larger proportion of the food present at each feeding site. With respect to the latter possibility, the feeding bouts of females are interrupted by supplantations at a substantially and significantly higher rate than those of males (Post 1978; Post et al. 1980), and this factor probably accounts for some, but not all, of the difference in feeding bout durations (see discussion in Post et al. 1980).

These factors are not mutually exclusive, and it is not possible to examine the independent contributions of each in this report; further work along these lines is in progress (see also Post et al. 1980). To gain some insight into the effects of the dietary differences between males and females on the difference in mean feeding bout duration, I have examined the distributions of feeding bouts for each of four different foods for each focal animal (Fig. 6).

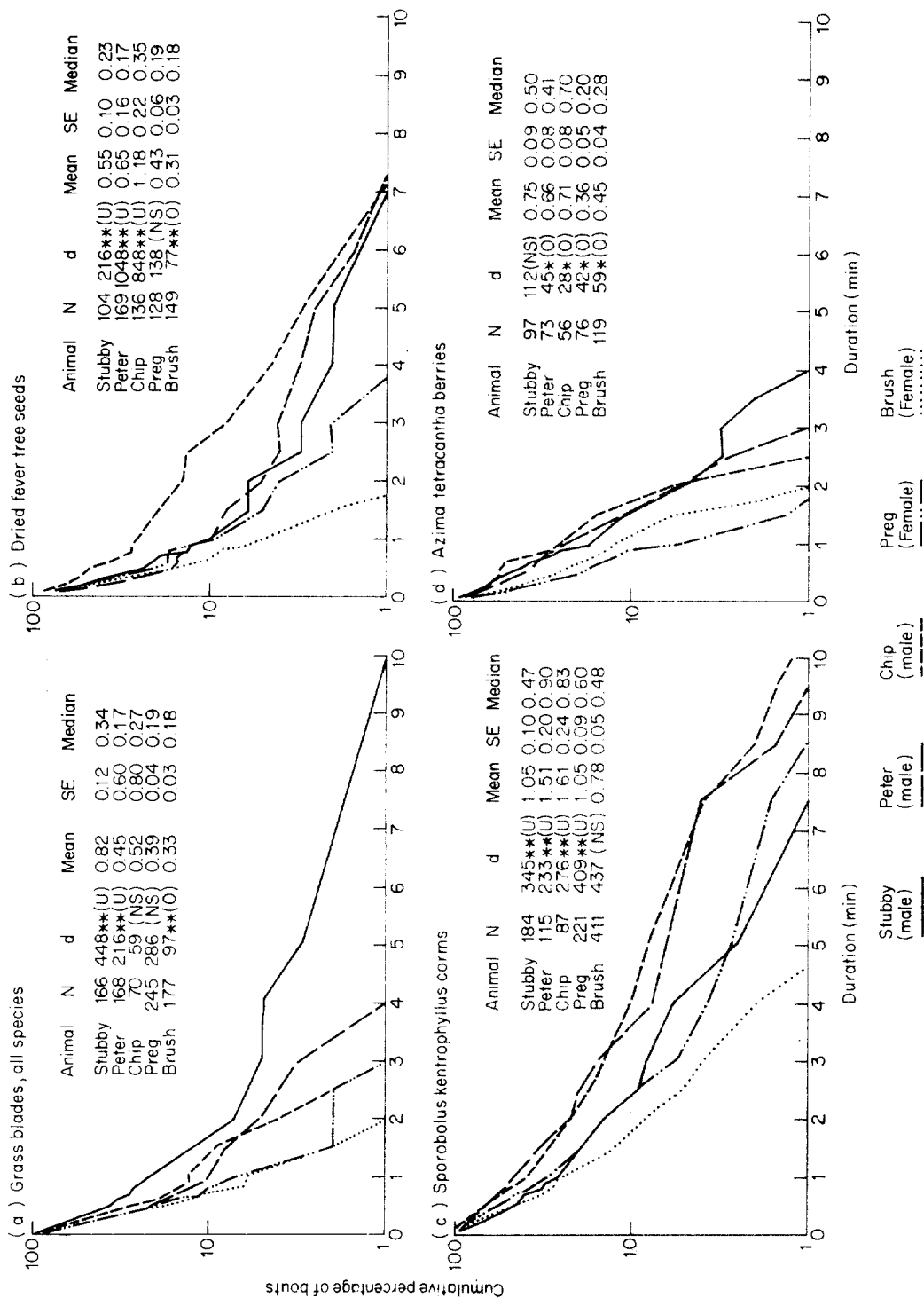


Fig. 6. Survivorship functions of feeding bout durations for the five focal animals on (A) grass blades, (B) dried seed pods of *Acacia xanthophloea*, (C) corms of *Sporobolus kentrophyllus*, and (D) berries of *Azima tetraacantha*. Ordinate scale is logarithmic. Also shown are the number of bouts ( $N$ ), the value of the dispersion statistic ( $d$ ), mean and median bout duration, and standard error of the mean (SE). Significance of the dispersion statistic is denoted as follows: \*\* =  $P < 0.01$ , \* =  $P < 0.05$ , NS = not significant. O = 'overdispersed', U = 'underdispersed'. See text for details.

The four foods chosen for this analysis were grass blades (all species), the dried seed pods of *Acacia xanthophloea*, the underground corms of *Sporobolus kentrophyllus*, and the berries of *Azima tetracantha*. Together these four foods accounted for just under 40% of the time spent feeding by the combined sample of individuals during this study (Post 1978, Tables 56 and 61). It should be pointed out that only feeding bouts during which the subject fed on a single food type were included in these analyses; since feeding bouts during which the subject switched from one food type to another were not uncommon, the total feeding time on any one food cannot be reconstructed from these data.

Tests of several hypotheses are shown in Table V. Differences in mean bout duration among the five individuals were significant for all four foods (Anova, Table V); a priori contrasts (Sokal & Rohlf 1969, page 226) between the mean bout durations of males and females were also significant for all four foods (Table V). In all of these cases the male bouts lasted longer than the female bouts (Fig. 6).

For highly skewed distributions of this kind, the median may be a more appropriate measure of central tendency than the mean. Accordingly, medians for all distributions are displayed in Fig. 6, and the results of two versions of the

median test (Siegel 1956) in Table V. Differences in median bout duration among the five individuals were significant for all four foods (Table V); that is, the null hypothesis that the five samples are drawn from populations with the same median can be rejected in all cases. The hypothesis that the male and female medians are equal was tested by pooling all bouts for all individuals of each sex and comparing the two medians with the two-sample median test (Siegel 1956, page 111). This is not strictly appropriate since, as we have just seen, these samples are significantly heterogeneous. However, there is no analogue, for the median test, of the a priori contrasts used for means. For three of the four foods the difference between the male and female medians was significant (Table V). It should be noted that, in general, the differences between the male and female means are greater than the corresponding differences between the medians (Fig. 6); for example, the males' mean durations are always greater than or equal to the female mean durations, while the same is not true for the medians (see Fig. 6 and Discussion).

In addition to these differences in central tendency, there are characteristic differences in the dispersions of the male and female bout duration distributions. For each distribution the dispersion statistic  $d$  (Cox & Lewis 1966, page

Table V. Testing Interindividual and Intersexual Differences in Mean and Median Feeding Bout Durations

Source	ANOVA				Median test	
	<i>df</i>	Sum of squares	Mean squares	<i>F</i>	$\chi^2$	<i>df</i>
A. Grass blades						
Individuals	4	25.82	6.45	8.309**	20.24**	4
Sexes	1	13.26	13.26	17.076**	5.49*	1
Error	821	637.71	0.78			
B. <i>A. xanthophloea</i> seed pods						
Individuals	4	61.85	15.39	5.833**	21.95**	4
Sexes	1	30.81	30.81	11.676**	2.61 (ns)	1
Error	681	1797.23	2.64			
C. <i>S. kentrophyllus</i> corms						
Individuals	4	76.61	19.15	9.882**	41.36**	4
Sexes	1	42.01	42.01	21.661**	12.62**	1
Error	1013	1998.08	1.94			
D. <i>A. tetracantha</i> berries						
Individuals	4	9.75	2.44	5.782**	17.22**	4
Sexes	1	9.09	9.09	21.562**	17.34**	1
Error	415	174.99	0.42			

\* $P < 0.05$ . \*\* $P < 0.01$ .

158; Dienske & Metz 1977) was computed, defined as:

$$d = \frac{\sum_{i=1}^k (N_i - \bar{N})^2}{\bar{N}}$$

where  $N_1, N_2, \dots, N_k$  are the lengths of the  $k$  observed bouts and  $\bar{N} = \Sigma N_i/k$ . The  $d$  statistic is distributed as a  $\chi^2$  variate with  $k-1$  degrees of freedom under the null hypothesis that the  $N_i$ 's are sample observations of a Poisson variable, i.e. that bout termination rate is constant irrespective of bout length. The  $d$  statistic is closely related to the sample variance of the distribution under examination. In fact,  $d/(k-1)$  is simply the ratio of the estimated sample variance to the mean, and the dispersion test is roughly a comparison of this variance/mean ratio with its expected value of unity under the null (Poisson) hypothesis. Significantly high  $d$  values suggest that bout lengths are 'underdispersed', i.e. with a variance significantly higher than expected under the null hypothesis; low  $d$  values suggest 'overdispersion' or lower-than-expected variance.

The results of the dispersion tests are shown along with the distributions themselves in Fig. 6. The female feeding bout distributions tend either to fit the Poisson model (3/8) or to show overdispersion (4/8), while the male distributions are predominantly underdispersed (8/12). Ten of the 12 male distributions (83%) deviate significantly from the Poisson model, while 62.5% (5/8) of the female distributions do so; this difference is not significant (Fisher's Exact Test,  $P > 0.05$ ). However, the male distributions are significantly more likely to deviate from the Poisson model in the direction of underdispersion than are the female distributions (Fisher's Exact Test,  $P = 0.047$ ). Figure 6 shows that these underdispersed distributions tend to be convex to the origin, with long 'tails' signifying a decreasing rate of bout termination (see Dienske & Metz 1977).

In summary, these analyses have shown that the longer feeding bouts of the males (Fig. 5) are not simply the result of dietary differences between males and females, since differences in median and mean bout durations remain within single food types (Table V). Furthermore, there are significant differences between males and females in the variability of the feeding bout duration distributions that are reflected in the

different shapes of the distributions (above and Fig. 6; see Discussion).

The analysis of the moving bout distributions is somewhat less straightforward; moving bouts cannot be classified by food type as were feeding bouts, and can be classified only with reference to their end-points, which may be two feeding bouts on different foods, or two bouts of different activities. Comparison among individual distributions is difficult because of this underlying heterogeneity. However, certain differences between the male and female distributions (Fig. 7) are suggestive. Although the male means are significantly higher than the female means, there is no heterogeneity among the five sample medians ( $\chi^2 = 2.73$ ,  $df = 4$ ,  $P > 0.10$ ). The three male distributions are significantly underdispersed and are highly convex to the origin (Fig. 7), whereas neither of the female distributions shows either of these characteristics.

These results are surprising in that, as Deag (1977) has suggested, males would be expected to have shorter moving bouts, or shorter mean 'search times' for food, as a consequence of their higher dominance rank. Several hypotheses may account for this discrepancy: for example, males may require longer moving bouts to 'catch up' to the foraging group after it moves away during their longer feeding bouts. I suspect, however, that this discrepancy is due, in large part, to the fact that at least two different kinds of moving bouts have been lumped together in the distributions in Fig. 7: bouts between food plants within large food 'patches' and the (generally longer) bouts between food patches. These two types of moving bouts are often distinguished as separate activity categories, e.g. locomotion associated with feeding ('foraging') and loco-

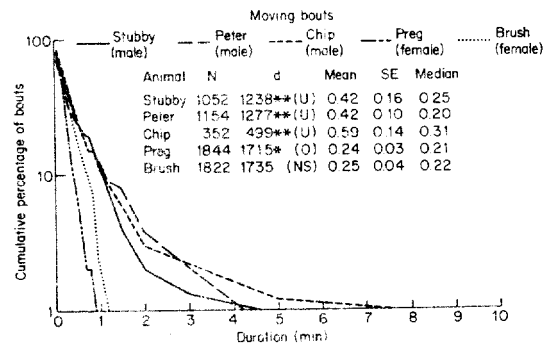


Fig. 7. Survivorship functions of moving bout durations for the five focal animals. Labels as in Fig. 6.

motion not associated with feeding ('travelling') (e.g. Rose 1977; Sussman 1977; Fleagle 1978), although I found that I was not able to distinguish consistently between these two types of locomotion (see Rose (1977) for a discussion of the intergradations of these activities). I suspect that the longer moving bouts of males are due to a larger number of these long 'travelling' bouts; a similar intersexual difference is suggested in Rose's data (1977, Table 8) on olive baboons, *Papio anubis*, where over one-quarter of the adult males' total time spent moving was spent in locomotion not associated with feeding, a figure substantially higher than the corresponding figures for females (5–17%).

As a preliminary attempt to examine this question further, I looked at only those moving bouts bounded on both sides by bouts of feeding on the most commonly eaten food, *Sporobolus kentrophyllus* corms. This is the only such classification that would yield reasonable sample sizes for all animals, and is used here to estimate the 'search time' within grassland food patches for each of the five animals. These distributions are shown in Fig. 8; note that due to the large number of short bouts (< 0.1 min) the scale of the abscissa in Fig. 8 is not the same as in Figs 6 and 7. There are no significant differences among the five animals with respect to either the means (Anova;  $F = 2.04$ ,  $df = 4, 429$ ,  $P > 0.10$ ) or medians ( $\chi^2 = 2.09$ ,  $df = 4$ ,  $P > 0.10$ ) of the distributions in Fig. 8. In addition, all distributions in Fig. 8 are significantly overdispersed. Although not a complete test of the hypothesis,

this analysis suggests that the longer moving bouts of males are not due to longer within-patch search times.

### Summary and Discussion

The major results of this study can be summarized as follows:

1. The proportions of time spent feeding and socializing vary significantly among the four seasons, and are inversely correlated with one another.

2. Significant interindividual variability was detected in the proportions of time spent feeding, moving, and socializing among the five focal animals. None of the observed intersexual differences in activity proportions were significant.

3. No direct effect of environmental variability (rainfall, temperature) on the mean proportion of time spent in each activity state could be detected.

4. Examination of the distribution of feeding bout lengths showed that the feeding bouts of males are, on the average, longer than those of females and less consistent than those of females with a model of the random termination of bouts. Male feeding-bout-length distributions tend to be 'underdispersed', in contrast to the 'overdispersion' of the female distributions. These differences remain after controlling for possible differences due to intersexual dietary differences.

5. Moving bouts of males are longer than those of females, and the results are consistent with the hypothesis that a higher proportion of male moving bouts involve long travelling between widely spaced food patches.

6. Day-to-day variability in the amount of time spent in each activity state during each hour of the day is quite high, and a surprisingly small number of significant diurnal patterns could be detected.

Moving bouts between *S. kentrophyllus* corms

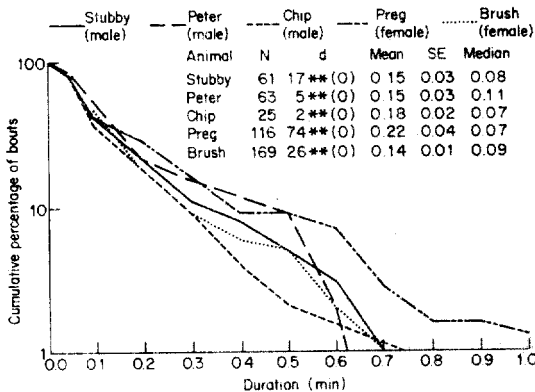


Fig. 8. Survivorship functions of the durations of moving bouts bounded on both sides by bouts of feeding on the corms of *Sporobolus kentrophyllus*. Note the change in the scale of the abscissa. Labels as in Fig. 6.

### Activity Proportions: Seasonal Variability

A comparison of the results of this study with those of other studies of baboons is difficult, largely because of differences in sampling methodologies. It does appear that baboons inhabiting relatively open grassland spend more time feeding (40% to 50%) (*Papio cynocephalus*, this study; *P. anubis*, Harding 1976 and Rose 1977; *P. ursinus*, Hall 1962 and Davidge 1978) than baboons in more heavily forested environments (20% to 30%) (*P. anubis*, Crook & Aldrich-Blake 1968; Nagel 1973; Dunbar & Dunbar 1974). Whether this is due to the higher

nutritional quality of the fruits and flowers available to forest baboons remains to be determined. Where seasonal variability in the proportion of time spent feeding has been uncovered, baboons spend more time feeding during periods of low rainfall (this study; Nagel 1973; Davidge 1978); fluctuations in the nutritional quality of available foods are again a possible, but as yet unverified, cause of these seasonal differences (see below). These observations support Nagel's suggestion that 'baboon groups are highly flexible in their activity patterns and capable of adaptively responding to local and seasonal habitat variants' (Nagel 1973, page 139).

As Clutton-Brock (1977) has emphasized, seasonal variability in time budgets is less likely to be affected by climatic variation per se than by seasonal changes in food availability; therefore, unless the nature of seasonal variability in food availability is well understood, the presence or absence of variability in the proportion of time spent in different activity states may be difficult to interpret. Quantitative assessment of seasonal fluctuations in the total amount of food available to the Amboseli baboons was difficult, largely because of both the large number of different food species utilized by the baboons and the large size of Alto's group's home range (over 40 km<sup>2</sup>, Post 1978). Data presented elsewhere (Post 1978 and in preparation) suggest that overall food availability is lowest during the long dry season. During this period there was a decrease in the diversity of the baboons' diet, as over 40% of their feeding time was spent on grass corms, in addition to the increase in the proportion of time spent feeding discussed earlier (Table III). This increase during a period of presumed lowered food availability contrasts with studies of other primate species demonstrating a decrease, or no change, in the proportion of time spent feeding during such periods (e.g. *Colobus badius*, Clutton-Brock 1974; *Symphalangus syndactylus*, Chivers 1977; *Cercocebus galeritus*, Homewood 1978; *Propithecus verreauxi*, Richard 1977; *Alouatta villosa*, Smith 1977; *Cercocebus albigena*, Waser 1975). A possible explanation for this finding may be that the time required to harvest a given volume of food increases when underground corms make up a high proportion of the diet (see Harding 1976).

The proportions of time spent in the four activity states form a mutually dependent set, in that time spent in one activity is necessarily unavailable for the performance of others. As a result, the statistical significance of the negative

correlation between time spent feeding and socializing (p. 360) cannot be evaluated by the usual methods. I would suggest, nonetheless, that this inverse relationship may still have some behavioural significance. It should be noted that early morning and late afternoon socializing peaks ('social hours'; see Altmann & Altmann 1970) occurred only during those seasons with relatively low proportions of time feeding (short rains and inter-rains; Fig. 3 and Table III). Such an inverse relationship would be expected where feeding time was a function of some exogenous variable(s) (e.g. the average nutritional quality or handling time of available food), with socializing time a function of feeding time. Of course, causation may flow in the reverse direction, with exogenously imposed variability in time spent socializing acting as a constraint on the amount of time available for feeding. This is unlikely, both because several studies have shown that feeding takes precedence over social activities during periods of extremely low food availability (Hall 1962; Loy 1970) and because the Amboseli baboons do not show pronounced mating seasons during which the time spent in social behaviours might be expected to increase irrespective of food availability at that time. However, the existence of this constraint on socializing time cannot be demonstrated unambiguously with these data. Thus it is difficult to assess the significance of, for example, the contrast between the Amboseli baboons and the *Papio anubis* population studied by Nagel (1973), where 'increases in feeding go at the cost of resting', not socializing, on both a seasonal and diurnal basis (Nagel 1973, page 147).

It is perhaps noteworthy that the general pattern of seasonal variability reported for this study corresponds quite closely to data obtained during the next year (1975-76) by J. Altmann on seasonal variability in the proportion of time that the members of this same group spent feeding and moving (J. Altmann 1980, Fig. 10). In both studies there was a marked peak in the proportion of time spent moving during November through January (short rains), with relatively low feeding percentages at this time, and high feeding percentages during the dry season, suggesting that these gross patterns, at least, are relatively constant from year to year.

#### Activity Proportions: Individual Variability

We might expect adult males to spend a higher proportion of their time feeding than adult females: their maintenance metabolic require-

ments are certainly higher due to their larger size, and the energetic costs of their activity appear to be higher as well (Coelho 1974; Coelho et al. 1979). That they do not do so appears to be the rule, rather than the exception, even among highly dimorphic species (see reviews in Clutton-Brock (1977) (primates) and Leuthold (1977), page 62 (ungulates)). While our data (Post 1978; Post et al. 1980) suggest that adult males and females ingest individual food items at similar rates (see also Rhine & Westlund 1978), several other factors may be involved, including possible male priority of access to high-quality feeding sites (Deag 1977; Dittus 1977; Post et al. 1980) and the increased metabolic demands of pregnancy and lactation in females (Payne & Wheeler 1968; Widdowson 1977; Demment 1978; J. Altmann 1980; Post 1980). The direct effects of each of these factors on activity budgets remain to be determined.

### Diurnal Distribution of Activity

Insofar as the adaptive significance of diurnal variability in primate activity budgets is only poorly understood (Clutton-Brock 1977), it is difficult to interpret the absence of significant diurnal patterns in *P. cynocephalus*. Biphasic or triphasic feeding patterns, with early or mid-morning and mid- or late-afternoon feeding peaks, have been commonly reported among arboreal species (see reviews in Clutton-Brock 1977, page 548, and Rose 1974, page 202). In contrast, the large-bodied, terrestrial primates generally display less marked diurnal variation, with feeding, in particular, occupying a relatively constant proportion of the daylight hours with the exception of an hour or so in early morning and late afternoon (*Papio anubis*, Aldrich-Blake et al. 1971; Nagel 1973; Harding 1976; Rose 1977; *Papio ursinus*, Davidge 1978 and Hall 1962; *Theropithecus gelada*, Crook & Aldrich-Blake 1968; Dunbar & Dunbar 1974; Iwamoto 1975). While the results from this study tend to conform to the second pattern, as expected (see Altmann & Altmann 1970, page 94), it should be noted that the technique of combining data from different days may obscure the existence of activity peaks if day-to-day variability in the timing of those peaks is high (Aldrich-Blake et al. 1971; Clutton-Brock 1974; Schlichte 1978); this appears to be the case here (Fig. 3). Nonetheless, any relationship between the animals' activity and either clock time or activity during a previous interval is a weak one.

Although numerous factors are presumably involved as determinants of diurnal activity patterns, including diurnal variability in temperature and solar insolation (Chivers 1968, 1977; Jarman & Jarman 1973; Lewis 1975; Richard 1977) and digestive physiology and morphology (Leuthold 1977, page 61 ff.), I would suggest that home range size as well as resource dispersion and predictability are involved as well. It may be difficult for animals within highly mobile species such as *P. cynocephalus*, with long day-journeys and large home ranges (Altmann & Altmann 1970; Post 1978), to adhere to an invariant diurnal activity pattern due to the difficulty of consistently finding suitable areas for periods of intensive feeding or resting at specific times of day within the context of an efficient overall foraging pattern. Critical environmental resources, such as sleeping sites, waterholes, and food 'patches', are both highly clumped and dispersed over an extremely large area (S. Altmann 1974; Slatkin 1975); animals such as the Amboseli baboons, and others facing similar resource distributions, may face particularly difficult 'scheduling' problems compared to animals facing more uniform resource distributions in smaller home ranges. The adaptive strategy in such circumstances may involve a high degree of behavioural flexibility with respect to the timing of periods of intense activity; groves of shade-producing trees may be sufficiently dispersed, and the location of abundant food resources sufficiently distant and unpredictable, that adherence to a fixed schedule is not possible. This distribution may be, in part, responsible for the general absence of conspicuous diurnal patterns in this and other large-bodied terrestrial species with their characteristically long day-journeys and large home ranges.

### Duration of Activity Bouts

Many of the differences between the male and female feeding and moving bout distributions can be attributed to an excess of longer-than-expected bouts by males. This is reflected in (a) generally greater intersexual differences between means than between medians (Figs 6-8, Table V), the mean being more sensitive to extreme observations, and (b) the underdispersion and longer 'tails' of the male distributions (Figs 6-8). I have presented evidence (p. 369) suggesting that male moving bout distributions contain a relatively high proportion of long, between-patch 'travelling' bouts. I would further suggest that the differences in feeding bout durations reflect

differences between males and females in the extent to which they are affected by within-group competition for food.

Competition for food may be either direct, involving threat or physical attack resulting in supplantations at feeding sites, or indirect, involving the decrease in 'effective' food patch size and density resulting from the simultaneous or sequential feeding of several animals in the same patch (see S. Altmann 1974; Dittus 1977; Slatkin & Hausfater 1977; Post et al. 1980). We have demonstrated that adult males are supplanted from feeding sites significantly less frequently than adult females (Post 1978; Post et al. 1980), presumably as a consequence of their higher dominance rank (see Hausfater 1975). However, we have also shown that this relationship alone is unlikely to account for all inter-individual or intersexual differences in the distribution of feeding bout durations (Post et al. 1980). These differences may therefore additionally reflect the effects of indirect competition on foraging animals.

Slatkin & Hausfater (1977) have suggested that solitary males, spatially removed from the main body of the foraging group, have longer feeding bouts than group-living males as a result of their relative immunity from this indirect competition. Analogously, differences in spatial deployment between males and females within the foraging group may underlie the intersexual differences in feeding bout distributions described in this report. The three adult males in this sample often fed for long periods of up to several hours while apparently out of visual contact with other group members; neither of the females ever did so. Dietary differences between the sexes reflect this difference in foraging patterns: males spent significantly more time feeding on the gum of the fever tree, a highly dispersed and unpredictable food source found primarily on the periphery of the group's range, while females spent more time feeding on grass corms, an abundant, predictable, and uniformly distributed food (Post 1978 and in preparation).

In short, the two sexes may be employing somewhat different resource exploitation strategies. The ratio of costs to benefits for each strategy may differ depending on an individual's sex, dominance rank, and age; different behavioural profiles may therefore result even if each individual chooses its 'optimal' strategy (see Bertram 1978; Demment 1978). One strategy, associated primarily with adult males, entails periods of more or less independent foraging at

relatively great distances from other group members. The benefits of such a strategy include the avoidance of both direct and indirect competition for food, which in turn leads to a higher probability of finding large, unexploited food patches. Potential costs are more difficult to assess; males engaged in such foraging excursions often had to 'backtrack' if the future course of group movement had been misjudged, thereby incurring extra energetic costs, and often no suitable feeding sites were actually located. In addition, such excursions presumably increase an individual's chances of being attacked by a predator, although in the absence of more direct evidence that remains no more than a plausible hypothesis.

An alternative strategy, associated primarily with adult females, is somewhat more conservative and entails the maintenance of relatively close proximity to other members of the foraging group. The primary benefit here is likely to be greater predictability of locating suitable feeding sites, since the group as a whole is likely to be foraging in areas of relative abundance. The primary cost is heightened competition for feeding sites and the decreased likelihood of finding large, unexploited food patches. This necessitates more frequent (but shorter) moving bouts between feeding sites of moderate abundance, and shorter (but less variable) feeding bouts.

The cost/benefit ratio of the first strategy may be lower for males than for females because of (a) the males' larger size, which may make a fatal predatory encounter less likely, (b) the females' need to conserve energy during pregnancy and lactation and their unwillingness to pursue a strategy with highly variable returns, or (c) the risks for low-ranking animals of being supplanted from a valuable food source requiring large inputs of time and energy to locate. It should be emphasized that the above represent a series of hypotheses to be tested in future work. Such tests will require data on, for example, the relationship between proximity to other animals and likelihood of an encounter with predators, the density of animals in proximity as a function of age and sex, and the energetic consequences of different exploitation strategies. Hopefully such work will contribute to our understanding of the nature of within-group competition for food and of the differential responses of individuals to that competition.

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#### REFERENCES

- Aldrich-Blake, P., Bunn, T., Dunbar, R., & Headley, P. 1971. Observations on baboons, *Papio anubis*, in an arid region in Ethiopia. *Folia Primat.*, **15**, 1-35.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227-267.
- Altmann, J. 1980. *Baboon Mothers and Infants*. Cambridge, Mass.: Harvard University Press.
- Altmann, J., Altmann, S., Hausfater, G. & McCuskey, S. 1977. Life history of yellow baboons: physical development, reproductive parameters, and infant mortality. *Primates*, **18**, 315-330.
- Altmann, S. 1974. Baboons, space, time, and energy. *Am. Zool.*, **14**, 221-248.
- Altmann, S. & Altmann, J. 1970. *Baboon Ecology*. Chicago: University of Chicago Press.
- Bernstein, I. 1976. Activity patterns in a sooty mangabey group. *Folia Primat.*, **26**, 185-206.
- Bertram, B. C. R. 1978. Living in groups: predators and prey. In: *Behavioural Ecology* (Ed. by J. R. Krebs & N. B. Davies), pp. 64-96. Sunderland, Mass.: Sinauer Associates.
- Chivers, D. 1968. On the daily behaviour and spacing of howling monkey groups. *Folia Primat.*, **10**, 48-102.
- Chivers, D. 1977. The feeding behaviour of siamang (*Symphalangus syndactylus*). In: *Primate Ecology* (Ed. by T. H. C. Clutton-Brock), pp. 355-383. New York: Academic Press.
- Clutton-Brock, T. H. C. 1974. Activity patterns of red colobus (*Colobus badius tephrosgeles*). *Folia Primat.*, **21**, 161-187.
- Clutton-Brock, T. H. C. 1977. Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In: *Primate Ecology* (Ed. by T. H. C. Clutton-Brock), pp. 529-536. New York: Academic Press.
- Clutton-Brock, T. H. C. & Harvey, P. 1977. Species differences in feeding and ranging behaviour in primates. In: *Primate Ecology* (Ed. by T. H. C. Clutton-Brock), pp. 557-584. New York: Academic Press.
- Coelho, A. 1974. Socio-bioenergetics and sexual dimorphism in primates. *Primates*, **15**, 263-269.
- Coelho, A., Bramblett, C. & Quick, L. 1979. Activity patterns in howler and spider monkeys: an application of socio-bioenergetic methods. In: *Primate Ecology and Human Origins* (Ed. by I. S. Bernstein & E. O. Smith), pp. 175-200. New York: Garland STPM Press.
- Cox, D. & Lewis, H. 1966. *The Statistical Analysis of a Series of Events*. London: Methuen.
- Crook, J. H. & Aldrich-Blake, P. 1968. Ecological and behavioural contrasts between sympatric ground dwelling primates in Ethiopia. *Folia Primat.*, **8**, 192-227.
- Davidge, C. 1978. Activity patterns of chacma baboons (*Papio ursinus*) at Cape Point. *Zool. Afr.*, **13**, 329-350.
- Davis, R. T., Leavy, R. W., Smith, M. D. C. & Thompson, R. F. 1968. Species differences in the gross behaviour of nonhuman primates. *Behaviour*, **31**, 326-338.
- Deag, J. 1977. Aggression and submission in monkey societies. *Anim. Behav.*, **25**, 465-474.
- Demment, M. 1978. Nutritional constraints on the evolution of body size in baboons. Paper presented at the Wenner-Gren Symposium 'Baboon Field Research'.
- Dienske, H. & Metz, H. A. J. 1977. Mother-infant body contact in macaques: time interval analysis. *Biol. of Behav.*, **2**, 3-37.
- Dittus, W. 1977. The social regulation of population density and age-sex distribution in the toque monkey. *Behaviour*, **63**, 281-322.
- Dunbar, R. & Dunbar, P. 1974. Ecological relations and niche separation between sympatric terrestrial primates in Ethiopia. *Folia Primat.*, **21**, 36-61.
- Fleagle, J. 1978. Locomotion, posture, and habitat use of two sympatric leaf-eating monkeys in West Malaysia. In: *Recent Advances in Primatology Vol. I* (Ed. by D. Chivers & J. Herbert), pp. 331-336. London: Academic Press.
- Gaulin, S. 1979. A Jarman/Bell model of primate feeding niches. *Hum. Ecol.*, **7**, 1-20.
- Hall, K. R. L. 1962. Numerical data, maintenance activities and locomotion in the wild chacma baboon (*Papio ursinus*). *Proc. zool. Soc. Lond.*, **139**, 181-220.
- Harding, R. S. O. 1976. Ranging patterns of a troop of baboons (*Papio anubis*) in Kenya. *Folia Primat.*, **25**, 143-185.
- Hausfater, G. 1975. Dominance and reproduction in baboons: a quantitative analysis. *Contrib. Primat.*, **7**, 1-150.
- Homewood, K. 1978. Feeding strategy of the Tana mangabey (*Cercocebus galeritus galeritus*). *J. Zool.*, **186**, 375-391.
- Iwamoto, T. 1975. Food resource and the feeding activity. *Proc. Fifth Int. Congr. Primat.*, 475-481.
- Jarman, M. V. & Jarman, P. 1973. Daily activity of impala. *E. Afr. Wildl. J.*, **11**, 75-92.
- Kaplan, E. L. & Meier, P. 1958. Nonparametric estimates from incomplete observations. *J. Am. Stat. Assoc.*, **53**, 456-481.
- Leuthold, W. 1977. *African Ungulates*. Berlin: Springer-Verlag.

- Lewis, J. G. 1975. A comparative study of the activity of some indigenous East African ungulates and conventional stock under domestication. Ph.D. thesis, University of London.
- Loy, J. 1970. Behavioral responses of free-ranging rhesus monkeys to food shortage. *Am. J. Phys. Anthropol.*, **33**, 263-271.
- Nagel, U. 1973. A comparison of anubis baboons, hamadryas baboons, and their hybrids at a species border in Ethiopia. *Folia Primat.*, **19**, 104-165.
- Payne, P. R. & Wheeler, E. F. 1968. Comparative nutrition in pregnancy and lactation. *Proc. Nutr. Soc.*, **27**, 129-138.
- Post, D. 1978. Feeding and ranging behavior of the yellow baboon (*Papio cynocephalus*). Ph.D. thesis, Yale University.
- Post, D. 1980. Sexual dimorphism in the anthropoid primates: some thoughts on causes and correlates. In: *Sexual Dimorphism in the Primates* (Ed. by C. Eastman & P. Heisler). New York: Garland STPM Press.
- Post, D. In preparation. Feeding behavior of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya.
- Post, D., Hausfater, G. & McCuskey, S. 1980. Feeding behavior of yellow baboons (*Papio cynocephalus*): relationship to age, gender, and dominance rank. *Folia Primat.*, **34**, 170-195.
- Rhine, R. & Westlund, B. 1978. The nature of a primary feeding habit in different age-sex classes of yellow baboons (*Papio cynocephalus*). *Folia Primat.*, **30**, 64-79.
- Richard, A. 1977. The feeding behaviour of *Propithecus verreauxi*. In: *Primate Ecology* (Ed. by T. H. C. Clutton-Brock), pp. 72-96. New York: Academic Press.
- Rose, M. D. 1974. Postural adaptations in Old World monkeys. In: *Primate Locomotion* (Ed. by F. Jenkins), pp. 201-222. New York: Academic Press.
- Rose, M. D. 1977. Positional behaviour of olive baboons (*Papio anubis*) and its relationship to maintenance and social activities. *Primates*, **18**, 59-116.
- Rowell, T. 1966. Forest-living baboons in Uganda. *J. Zool.*, **149**, 344-364.
- Schlichte, W. 1978. A preliminary report on the habitat utilization of a group of howler monkeys in the National Park of Tikal, Guatemala. In: *Ecology of Arboreal Folivores* (Ed. by G. Montgomery), pp. 551-560. Washington: Smithsonian Press.
- Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.
- Slatkin, M. 1975. A report on the feeding behavior of two East African baboon species. In: *Contemporary Primatology* (Ed. by S. Kondo), pp. 418-422. Basel: S. Karger.
- Slatkin, M. & Hausfater, G. 1977. A note on the activities of a solitary male baboon. *Primates*, **17**, 311-322.
- Smith, C. 1977. Feeding behaviour and social organization in howling monkeys. In: *Primate Ecology* (Ed. by T. H. C. Clutton-Brock), pp. 97-127. New York: Academic Press.
- Snedecor, G. & Cochran, W. 1967. *Statistical Methods* (6th Edn). Ames, Iowa: Iowa State University Press.
- Sokal, R. & Rohlf, F. 1969. *Biometry*. San Francisco: W. H. Freeman.
- Struhsaker, T. T. 1967. Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli Game Reserve, Kenya. *Ecology*, **48**, 891-904.
- Struhsaker, T. T. & Leland, L. 1979. Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. *Adv. Stud. Behav.*, **9**, 159-228.
- Sussman, R. 1977. Feeding behaviour of *Lemur catta* and *Lemur fulvus*. In: *Primate Ecology* (Ed. by T. H. C. Clutton-Brock), pp. 1-37. New York: Academic Press.
- Waser, P. 1975. Monthly variations in the feeding and activity patterns of the mangabey, *Cercocebus albigena*. *E. Afr. Wildl. J.*, **13**, 249-265.
- Western, D. 1972. The structure, function, and dynamics of the Amboseli ecosystem. Ph.D. thesis, University of Nairobi.
- Widdowson, E. 1977. Changes in the body and its organs during lactation: nutritional implications. In: *Breast Feeding and the Mother* (CIBA Symposium No. 45). Amsterdam: Elsevier.

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