

Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living

Lynne A. Isbell¹ and Truman P. Young²

¹ Department of Anthropology, Rutgers University, Douglass Campus, Box 270, New Brunswick, NJ 08903 USA

² Louis Calder Center, Fordham University, Drawer K, Armonk, NY 10504 USA

Received June 30, 1992 / Accepted in revised form February 17, 1993

Summary. Activity patterns were documented over a 20-month period in six groups of vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. Group size varied both among groups and within groups through time. The home ranges of two groups were located in *Acacia xanthophloea* habitat whereas those of four adjacent groups were located in *A. tortilis* habitat. Repeated measures analysis of variance, three-way analysis of variance, and meta-analysis of group size effects were carried out on feeding, moving, resting, scanning, allo-grooming, and 'other' behavior. Time spent feeding varied seasonally, peaking during periods when *A. tortilis* seeds were eaten. However, time spent feeding did not vary within or among groups, or between habitats, males and females, or dominants and subordinates. Males spend more time scanning and less time allo-grooming than females, and high-ranking individuals of both sexes spent more time scanning than low-ranking individuals. Among females, subordinates spent more time moving, whereas among males, dominants spent more time moving. Groups living in *A. xanthophloea* habitat spent more time moving and allo-grooming than groups in *A. tortilis* habitat but this may have been confounded by the fact that these two groups were on average larger than the others. Significant differences in activity budgets among groups demonstrate that activity patterns observed in one group are not always readily generalized to other groups even when they come from the same population. Group size analyses examined potential costs and benefits of group living. Increased intra-group competition, measured by time spent moving and feeding, was only weakly evident in larger groups. Individuals in larger groups allo-groomed more than individuals in smaller groups. Self-grooming also increased in larger groups. Individuals in larger groups spent less time scanning than individuals in smaller groups, but there was more scanning per group in larger groups than in smaller groups.

Introduction

Data on activity patterns are central to testing hypotheses about ecological influences on social behavior and group living. Activity budgets have been included as part of basic natural history for many group-living primate species, including saddleback tamarins (*Saguinus fuscicollis*: Terborgh 1983), mantled howler monkeys (*Alouatta palliata*: Milton 1980), wedge-capped capuchins (*Cebus olivaceus*: de Ruiter 1986), savannah baboons (*Papio cynocephalus*: Post 1981), red colobus (*Colobus badius*: Struhsaker 1975; Marsh 1981), capped langurs (*Presbytis pileata*: Stanford 1991), and mountain gorillas (*Gorilla gorilla*: Watts 1988). Most studies of activity budgets have shown that the time spent in different activities can vary both diurnally and seasonally within groups. They have also shown that activity patterns often differ between males and females, between dominants and subordinates, and between groups in different habitats.

The number of individuals in a group may also affect activity budgets. Group size effects have become more relevant as theoretical interest in the costs and benefits of group living has gained prominence (Pulliam 1973; Waser 1977; Hoogland 1979; Bertram 1980; Wrangham 1980; van Schaik 1983; de Ruiter 1986; Cheney and Seyfarth 1987; Robinson 1988; Isbell 1991; Isbell et al. 1991). For instance, in a number of animal species, scanning either remains the same or increases in larger groups, while individuals decrease the amount of time they themselves devote to vigilance [e.g., sparrows (*Passer domesticus*): Barnard 1980; starlings (*Sturnus vulgaris*): Powell 1974]. In many species, membership in groups is unstable, and the effect of group size on activities has been examined by comparing groups as they change in size. In contrast, because groups of primates tend to be stable in membership, the effect of group size on activities in primates has been examined largely by comparing groups of different sizes living in the same habitat (e.g., de Ruiter 1986; van Schaik et al. 1983). Comparisons of activity budgets within the same

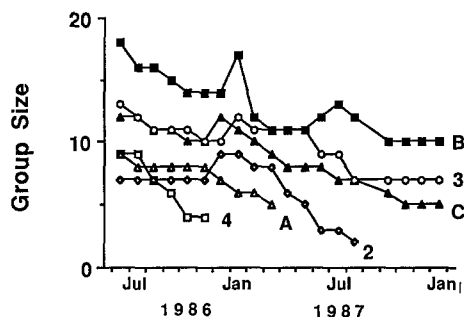


Fig. 1. Group sizes of the six vervet groups analyzed in this study. Solid symbols represent the two groups in *Acacia xanthophloea* woodland habitat, and the open symbols represent the four groups in *A. tortilis* woodland habitat. Three of the groups declined in size to such an extent that they fused with other groups before the end of the study and ceased to exist as separate groups

primate group as it changes in size over time have not been conducted (but see Watts 1988).

Here we examine the effects of sex, rank, habitat, and group size on activity budgets in six groups of vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya over a period of 20 months. Vervets live in savannahs, woodlands, and dry forests throughout subsaharan Africa (Wolfheim 1983). Within Amboseli, vervet groups occurred in both *Acacia xanthophloea* and *A. tortilis* habitats. *Acacia xanthophloea* is a fast-growing, short-lived tree that grows close to swamps and waterholes. In contrast, *A. tortilis* is a slow-growing, long-lived tree that grows in the absence of surface water. Although the six study groups lived in adjacent home ranges, two of the groups lived in *A. xanthophloea* habitat, whereas the other four groups lived in *A. tortilis* habitat.

Vervets typically live in multi-male, multi-female groups that vary in size from as few as two adults and accompanying immatures (Isbell et al. 1991) to as many as 75 individuals (Kavanagh 1981). In Amboseli, Struhsaker (1967) reported that group size averaged about 24 individuals in the early 1960s. Subsequent studies of the same population demonstrated that group size declined relatively slowly until mid-1986 (Strohsaker 1973, 1976; Cheney and Seyfarth 1987). Thereafter, numbers declined at a faster rate (Isbell 1990; Isbell et al. 1990); indeed, three of the six main study groups became sufficiently small that the remaining members joined neighboring groups and their own groups disintegrated (Isbell et al. 1991). By the end of 1987, group size averaged 9.5 for the three remaining groups (Fig. 1).

This was an ideal population in which to examine environmental and social influences on activities of individuals because (1) the environment was seasonal, (2) the habitat varied within the population, (3) group size varied among groups, and (4) group size varied within groups over a relatively short time.

Study site and methods

The study was conducted from May 1986 to August 1988 in Amboseli National Park, Kenya (37° 10' E, 2° 51' S). Amboseli is part

Table 1. Operational definitions of activities

Feeding:	manipulation or ingestion of food
Scanning:	gazing into the distance
Moving:	any form of locomotion
Allo-grooming:	inspection of another's fur or having one's fur inspected by another
Self-grooming:	inspection of one's own fur
Resting:	inactivity
Other:	any activity that was not covered by the other categories; included play, suckling one's infant, alarm-calling, and, after January 1987, self-grooming

of a semi-arid savannah ecosystem with two dry seasons yearly from about January through February and June to October (Struhsaker 1967; Western 1983). The research site within Amboseli was located in the southwestern corner of the park. Historically, the study site included both *A. xanthophloea* and *A. tortilis* (Struhsaker 1967; Western 1983). Within the last 30 years, however, woodlands of *A. xanthophloea* have declined dramatically. This decline has been attributed to browsing by elephants, an increase in the salinity of the soil (Western and Van Praet 1973), and senescence of even-aged trees, probably in combination (Young and Lindsay 1988). *Acacia xanthophloea* was once a primary source of food and shelter for vervets (Struhsaker 1967; Cheney et al. 1988). The vervet population decline resulted largely from decreased reproduction, but it was exacerbated in the short-term by increased predation (Cheney et al. 1988; Isbell 1990).

The six main study groups of vervets lived in contiguous home ranges that were defended against intrusions by neighboring groups. Two groups, B and C, occupied home ranges that included the last remaining *A. xanthophloea* in the area while the other four groups, A, 2, 3, and 4, occupied adjacent *A. tortilis* woodlands (see Isbell et al. 1990 for a more complete description of their habitats).

Systematic sampling of activities was undertaken from June 1986 through January 1988, except in September 1987. Point, or scan, samples (Altmann 1974) were collected on all subadults and adults (all females 3 years and older, and all males 5 years and older) engaged in the following activities: feeding, scanning, resting, moving, allo-grooming, and 'other', which included social and nonsocial behaviors. From June 1986 to February 1987, point samples of self-grooming were also collected. Thereafter, self-grooming was recorded only as an 'other' activity. Operational definitions are provided in Table 1. On occasion, animals fed and simultaneously engaged in another activity. Under these circumstances, feeding was given precedence and was scored over other activities.

From June 1986 to February 1987, point samples of the first activity of individuals were taken at 5-min intervals throughout the observation period with a given group. Sampling of individuals during this observation period followed a predetermined random order, with a different individual being sampled at each interval until all adult group members were sampled. If the target animal was not found within 2 min, the next animal on the list was sampled until the target animal was located. The time interval for sampling individuals was changed to increase sample size in February 1987. From February 1987 until February 1988, the entire group was scanned at 10-min intervals and the first observed activity was recorded for each individual found within a 1-min window of time. Groups were scanned from left to right to avoid attraction to obvious behaviors such as fighting.

Statistical analyses. The initial analyses are based on 17,972 data points recorded over 19 months. For each adult, the proportion of scans during which each activity was seen was calculated for each hourly interval for each month. Monthly means for each adult were then calculated by weighting the hourly values equally over all sampled hours. Monthly means, rather than individual data

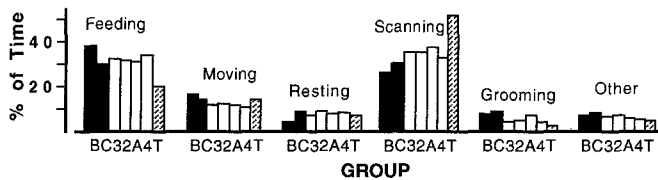


Fig. 2. Activity budgets of seven vervet groups, summed over all months and all individuals. The *solid bars* represent the *A. xanthophloea* groups (B and C) and the *open bars* represent the *A. tortilis* groups (3, 2, A, and 4). The *shaded bar* represents group TW3, a relatively unhabituated group into which A fused in March 1987. The first six groups are arranged in order of decreasing size within each habitat type (see Fig. 1)

points, were used as the unit of analysis to minimize problems associated with independence of data. Hourly values were weighted equally to avoid biases as a result of diurnal variation in activities. The resultant mean proportions were then arcsin transformed for statistical analysis ($n=650$ for each activity).

Months in which there were fewer than five observations for a particular individual were excluded for that individual. Individuals for which there were less than 3 months of data were also excluded. One of the main study groups, group A, fused in March 1987 with a group that had not been intensively studied (group TW3) (see Isbell et al. 1991). Group TW3 was relatively unhabituated. After fusion, the group spent most of its time scanning during researcher presence, and significantly more time scanning ($t=4.28$, $P<0.01$, 2-tailed) and less time feeding ($t=3.64$, $P<0.02$, 2-tailed) than the other groups (Fig. 2). It is likely that is greater scanning was a result of wariness toward researchers. The data from group TW3 were therefore excluded from further analyses. The final sample size per activity after these exclusions was 590.

Dominance hierarchies in vervets are linear and reflect priority of access to resources such as food and grooming partners (Seyfarth 1980; Wrangham 1981; Whitten 1983). Ranks were determined each month on the basis of supplants and approach-avoid interactions. Separate dominance hierarchies were constructed for males and females within each group.

Monthly variation in activity patterns was examined by repeated-measures analysis of variance. These tests were carried out on each activity across all months. Because sex was a common significant effect in the three-way ANOVAs, it was included as an interacting effect in these analyses.

To examine patterns among groups, between males and females, and between dominants and subordinates for each of the six activity categories, a series of three-way ANOVAs with interactions was carried out for each activity on values averaged over all months for each individual, with sex, rank, and group as the main effects ($n=54$ individuals). For 'rank', animals were assigned to either the upper or lower half of the dominance hierarchy in each group. Animals in the exact middle of a dominance hierarchy were assigned to the lower half.

The effects of group size on vervet activity budgets were examined both among groups in the same months and within groups over time. In these analyses, group size includes all group members except infants because previous studies suggested that juveniles,

but not infants, are similar to adults in their ability to detect predators (Seyfarth et al. 1980; Isbell et al. 1991), and this may influence scanning rates of the entire group. To compare differences among groups, Pearson correlation tests were conducted across months between group size and each activity for every month. The results were statistically summarized over all 19 months using a Fisher's combined test (Wolf 1986). Similarly, to compare differences within groups, Pearson correlation tests were conducted across months between group size and each activity for each group, and the results were statistically summarized over all six groups using a Fisher's combined test. Because time spent scanning per individual decreased significantly with group size, similar analyses were carried out on the product of group size and scanning time per individual to examine whether larger groups had a greater or lesser number of scanners per unit time than smaller groups. The mean regression coefficients were also calculated to allow an estimate of the relative contribution of additional individuals to group scanning. Although all data analyses were done on arcsin transformed data, means reported in the text are not transformed.

Results

Activity budgets

Figure 2 shows the average time that the groups spent feeding, moving, resting, scanning, allo-grooming, and in other activities. Between 30 and 40% of their time was spent feeding and a similar amount of time was spent scanning.

Monthly variation. The results of repeated-measures ANOVAs on temporal changes in activity for all groups are shown in Table 2. Significant monthly variation existed for all activities. The most striking difference is that, for all groups, vervets spent approximately twice as much time feeding in June through September as during other months ($F=13.85$, $P<0.01$; Fig. 3). This period coincided with a diet consisting almost exclusively of *A. tortilis* seeds (Isbell and Young, in preparation). The time spent in all other activities tended to decrease during the months of elevated feeding activity, with scanning in particular being inversely related to feeding across months (Fig. 3). 'Other' activities showed a significant sex by month interaction ($F=1.84$, $P<0.02$), with females but not males showing striking peaks in December 1986 and January 1987 and again in December 1987 and January 1988 (Fig. 4). This period coincided with the birth season and subsequent suckling of infants, which was scored as an 'other' activity.

Rank and sex differences. Results of three-way factorial ANOVAs on all six activities are presented in Table 3.

Table 2. Results of repeated-measures ANOVAs on six activity categories with respect to month and sex

Activity	Feeding		Moving		Resting		Scanning		Grooming		Other		
	df	F	P	F	P	F	P	F	P	F	P	F	P
Sex	1	0.48	0.49	0.11	0.74	0.16	0.69	8.55	0.004	31.24	<0.001	20.14	<0.001
Month	18	13.85	<0.001	4.25	<0.001	7.85	<0.001	5.11	<0.001	2.96	<0.001	4.89	<0.001
Sex × month	18	1.08	0.37	1.08	0.36	1.16	0.29	1.42	0.11	0.74	0.77	1.84	0.02

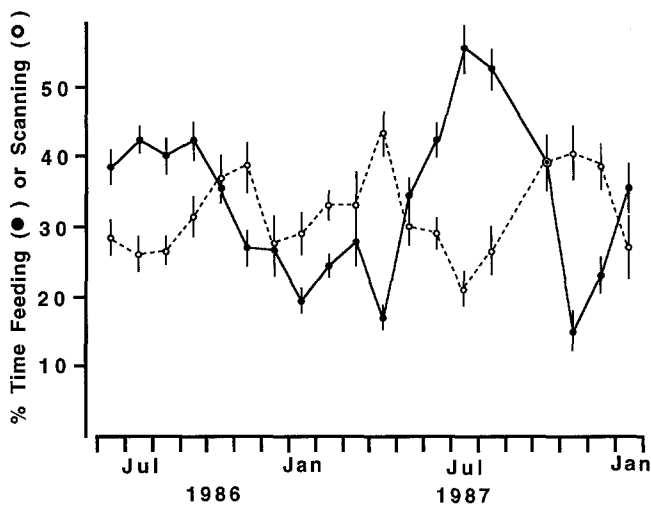


Fig. 3. Seasonal variation in time spent feeding (solid symbols) and scanning (open symbols), summed over all groups. Bars are ± 1 SE

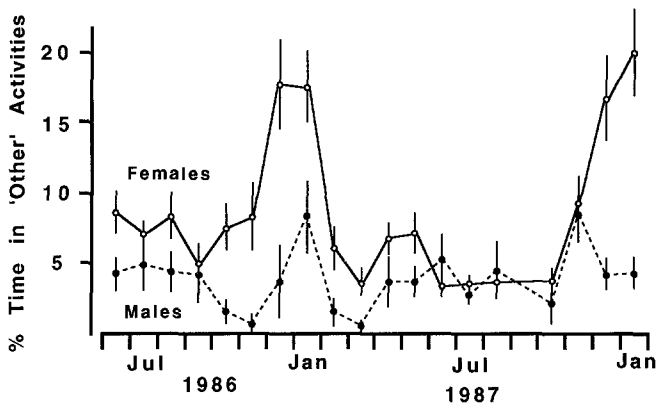


Fig. 4. Seasonal variation in 'other' behavior for females (solid symbols) and males (open symbols), summed over all groups. Bars are ± 1 SE

No significant differences existed between dominants and subordinates in feeding, moving, resting, allo-grooming, or 'other' behaviors. Dominants did spend significantly more time scanning than subordinates (means: 35.0% vs. 29.5%; $P=0.026$; Fig. 5).

No significant differences existed between males and females in feeding, moving, or resting (Table 3). Males

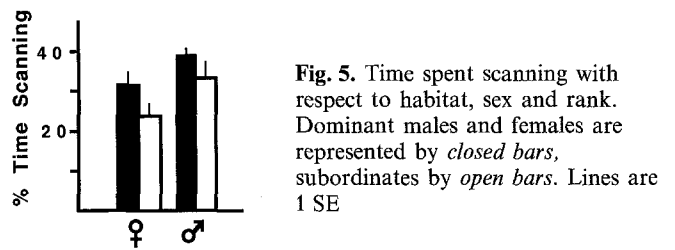


Fig. 5. Time spent scanning with respect to habitat, sex and rank. Dominant males and females are represented by closed bars, subordinates by open bars. Lines are ± 1 SE

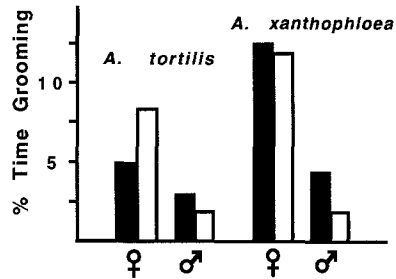


Fig. 6. Time spent allo-grooming with respect to habitat, sex and rank. Dominant males and females are represented by closed bars, subordinates by open bars

spent significantly more time scanning than females (means: 36.8% vs. 28.7%; $P=0.003$; Fig. 5). Females spent more time than males engaged in allo-grooming, either as groomers or recipients of grooming (means: 9.2% vs. 2.7%; $P<0.001$; Fig. 6) and in 'other' activities (means: 8.4% vs. 4.1%; $P<0.001$; Fig. 4).

There was a significant interaction between sex and rank with respect to allo-grooming ($P<0.001$, Fig. 6) and moving ($P=0.015$, Fig. 7). Among females, subordinates spent more time in allo-grooming (means: 10.0% vs. 8.2%) and more time moving than dominants (means: 14.7% vs. 12.7%), whereas among males, the opposite was true (allo-grooming means: 1.9% vs. 3.5%; moving means: 10.5% vs. 12.5%). However, groups differed significantly in the relationship among sex and dominance with respect to allo-grooming ('Group \times Sex \times Rank' interaction, $P=0.002$). Specifically, in group B, dominants spent more time involved in allo-grooming than subordinates among females (13.3% vs. 11.1%), and in group 2, dominants spent less time in allo-grooming than subordinates among both males (1.5% vs. 2.4%) and females (5.7% vs. 9.0%).

Table 3. Results of three-way factorial ANOVAs on six activity categories with respect to group, sex, and rank. This is a Model I ANOVA (see Sokal and Rohlf 1981, p. 383, for details)

Activity	Effect	df	Feeding		Moving		Resting		Scanning		Grooming		Other	
			F	P	F	P	F	P	F	P	F	P	F	P
Group		5	1.43	0.24	4.00	0.007	1.55	0.20	1.79	0.14	9.84	<0.0001	1.04	0.41
Sex		1	0.41	0.52	1.89	0.18	1.96	0.17	10.31	0.003	129.34	<0.0001	13.95	0.001
Group \times sex		5	1.25	0.31	0.33	0.89	1.22	0.32	2.03	0.10	3.44	0.014	1.90	0.12
Rank		1	1.82	0.19	0.17	0.68	0.25	0.62	5.50	0.026	1.60	0.22	0.38	0.54
Group \times rank		5	0.30	0.91	0.47	0.79	1.01	0.42	0.72	0.61	5.10	0.002	1.68	0.17
Sex \times rank		1	0.54	0.47	6.71	0.015	2.44	0.13	0.16	0.69	24.09	<0.0001	0.27	0.60
Group \times sex \times rank		5	1.06	0.40	1.21	0.32	1.77	0.15	1.34	0.28	4.81	0.002	1.10	0.38

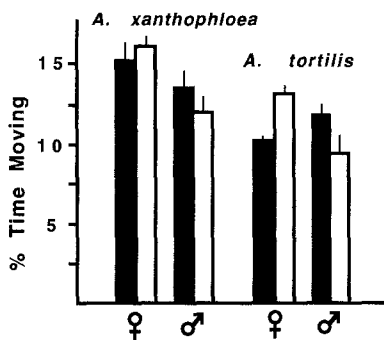


Fig. 7. Time spent moving with respect to habitat, sex and rank. Dominant males and females are represented by closed bars, subordinates by open bars. Lines are 1 SE

General patterns among groups. There were no significant differences among groups in time spent feeding, resting, or scanning. There were, however, significant differences among groups in time spent allo-grooming ($P < 0.001$; Fig. 6) and moving ($P = 0.007$; Fig. 7). Groups B and C, the two groups whose home ranges included the last remaining *A. xanthophloea* trees, spent more time allo-grooming (means: 8.6% vs. 5.0%) and moving (means: 14.7% vs. 11.4%) than the other groups.

Groups differed significantly in their sexual patterns of allo-grooming ('Group \times Sex' interaction; $P < 0.001$): the strongest sex difference occurred in group B (males = 2.3%; females = 11.9%) and the weakest in group 3 (males = 2.4%; females = 6.1%). Groups also varied in their relationships between dominance and allo-grooming ('Group \times Rank' interaction; $P = 0.002$). In Groups B and C (the *A. xanthophloea* groups), dominants spent somewhat more time involved in allo-grooming than subordinates (means: 8.9% vs. 8.5%; Fig. 6), whereas in the other (*A. tortilis*) groups the opposite was true, with subordinates spending 45% more time allo-groom-

ing than dominants (means, subordinates: 5.8% vs. dominants: 4.0%).

Group size and activity budgets

Among-group variation. The results of group size analyses are presented in Table 4. Although individuals in larger groups tended to spend more time feeding, resting, or engaged in 'other' activities, these differences were not significant (all values: $0.05 < P < 0.20$). For the latter category, the relationship becomes significantly positive ($P = 0.03$) if the 5 months with elevated levels (mostly due to suckling) are excluded, with larger groups spending more time in 'other' activities. This is mainly due to self-grooming; in the non-suckling months of June through October 1986 (the only non-suckling months during which self-grooming was recorded separately), 74% of all 'other' scores were of self-grooming. Larger groups spent significantly more time moving ($P < 0.005$) and involved in allo-grooming ($P < 0.005$) than smaller groups. Individuals in larger groups scanned significantly less than smaller groups ($P < 0.005$). Although individuals in larger groups scanned less, larger groups had significantly more scanners per unit time than smaller groups ($P < 0.001$). On average, each additional individual added 0.18 scanners per unit time (mean regression coefficient).

Within-group variation. As groups decreased in size, time spent resting ($P < 0.001$), allo-grooming ($P < 0.01$), and in 'other' activities ($P < 0.001$) decreased while scanning increased ($P < 0.001$). Although individuals scanned more as group size decreased, groups had significantly fewer scanners as they decreased in size ($P < 0.001$). On average, each additional individual added 0.19 scanners per unit time (mean regression coefficient). Individuals in larger groups tended to spend more time moving than those in smaller groups, but this difference was not significant ($P = 0.15$).

Table 4. Tests of the relationships between group size and six activity categories

Activity:	Within groups (across months)			Across groups (within months)			Groups with significant effects
	r_{mean}	χ^2	P	r_{mean}	χ^2	P	
Feeding	+0.06	17.4	0.15	+0.15	45.6	0.16	2 (-)
Moving	0.00	11.7	0.45	+0.41	64.8	<0.005	A (-)
Resting	+0.38	45.8	<0.001	+0.14	47.8	0.15	A, C, 2 (+)
Scanning	-0.35	37.8	<0.001	-0.35	69.4	<0.005	C (-)
Scanning times group size	+0.46	41.0	<0.001	+0.55	81.2	<0.001	2 (+)
Allo-grooming	+0.32	26.6	<0.01	+0.29	57.4	<0.025	A (+)
Other	+0.38	36.0	<0.001	+0.19	50.4	0.07	2, 4 (+)
E_{max} (less suckling months)	+0.64	50.0	<0.001	+0.37	43.8	0.03	A, B, 2, 3, 4 (+)

'Within groups' tests examined, for each group, the relationship between group size and activity across all months. 'Across groups' tests examined, for each month, the relationship between group size and activity across all groups. In the Fisher's combined test used here, the χ^2 values have $2n$ degrees of freedom (Wolf 1986). The 'within groups' analysis had 12 df (six groups), and the 'across groups' analysis had 38 df (19 months). There were 28 df

(14 months) for the 'across groups' analysis of 'other' behavior less months of peak suckling. Individual groups that showed a significant relationship between group size and a particular activity are listed. Group size is defined as the total number of adults, subadults and juveniles in a group (infants are excluded). Total sample size for each of these analyses was 632

Discussion

Feeding. There was remarkable consistency in time spent feeding across habitats, groups, sexes, and ranks. Adult male and female vervets of high and low rank spent statistically similar amounts of time feeding regardless of the size of their groups or the habitat in which they lived. Time spent feeding varied only across months, and almost certainly reflected changes in food resources (Isbell and Young, in preparation). Increased feeding times occurred during the seasons when the vervets' diet was limited almost entirely to *A. tortilis* seeds, which we suspect had much greater handling times than other foods because they are encased in pods that are not eaten. The consistency of feeding times between males and females contrasts with two of three groups of green monkeys studied in West Africa (*Cercopithecus aethiops sabaeus* and *C. a. tantalus*). Adult females spent less time feeding than adult males at Mt. Assirik, Senegal (Harrison 1983), more time feeding than males in Buffle Noir, Cameroon and similar amounts of time feeding in Kalamaloue, Cameroon (Kavanagh 1978). Our study implies that in Amboseli males and females were constrained to some level of feeding, and that other activities were adjusted to accommodate changes in seasonal demands on feeding. It is important to note that although all sex and rank classes in all groups spent similar amounts of time feeding, they may not have had the same diet or have eaten similar amounts of food, especially between the two different habitats (Isbell and Young, in preparation).

The consistency in feeding time across habitats contrasts also with studies of other primate species, e.g., ring-tailed and brown lemurs [*Lemur catta* and *L. fulvus* (Sussman 1977)] and Verreaux's sifaka [*Propithecus verreauxi* (Richard 1977)]. For example, red colobus in Kibale Forest, Uganda, spent 45% of their time feeding, whereas red colobus at the ecologically different Tana River, Kenya, spent only 30% of their time engaged in this activity (Struhsaker 1975; Marsh 1981). Mountain gorillas spent more time feeding when they were in areas of their home range with lower food biomass (Watts 1988).

Habitat effects. Habitat differences apparently did affect moving and allo-grooming and the relative amounts of time dominants and subordinates were involved in allo-grooming. Vervet groups in the *A. xanthophloea* habitat spent more time moving and allo-grooming than the groups in the *A. tortilis* habitat, and there was a significant tendency for dominants to groom more in the *A. xanthophloea* habitat. It is not surprising that differences in resource distribution or abundance can influence a group's daily movements (Clutton-Brock and Harvey 1977; Isbell 1991), but it is not clear how they might influence the time spent in allo-grooming or the proportionately greater time that dominants engaged in this activity. Although females groomed more than males in all groups, this cannot account for the pattern because groups living in the *A. xanthophloea* habitat did not have a higher ratio of females to males in their groups (*A.*

xanthophloea: 1.7; *A. tortilis*: 1.8), and in any case, sex was controlled for in the analysis of variance. Individuals in groups living in higher-quality habitats might have more time to groom because they were able to obtain foods more quickly than individuals in groups living in poorer quality habitats. However, this is also unlikely because the time spent feeding was not lower in these groups than in the other groups. Ectoparasite densities could be greater in the *A. xanthophloea* habitat, which could increase the time devoted to both allo-grooming and moving (to minimize exposure to infection). Alternatively, because the groups in *A. xanthophloea* habitat were larger on average than the groups in *A. tortilis* habitat, the greater allo-grooming levels in the former may have simply been a group size effect (allo-grooming times were significantly positively correlated with group size; see below).

Variation among groups. Despite the consistency in time spent feeding, the significant main group effects and the significant interaction effects of group identity, sex, and rank with respect to moving and allo-grooming (Table 3) highlight the fact that activity patterns observed in one group are not readily generalized to other groups, even when groups come from the same population (see also Lee 1983; Harcourt and Stewart 1984). The effect of local habitat differences and other, perhaps idiosyncratic, group differences in space and time can be significant. Long-term studies of multiple groups within a species may be necessary to fully document its 'characteristic' behavior.

Rank and sex differences in scanning. Males scanned more than females, and dominants scanned more than subordinates. Males may scan more than females because they must not only be aware of predators but must also be aware of other males attempting to join their group and gain access to females (Baldellou and Henzi 1992). Dominants may scan more than subordinates because they may have more relatives in their groups to protect from predators or they may be more involved in intergroup competition for resources (Cheney and Seyfarth 1985). These results are largely consistent with other studies of vervets. Baldellou and Henzi (1992) reported similar results from a population of vervets in South Africa. Cheney and Seyfarth (1981) found in an earlier study of the Amboseli population that dominant males spent more time scanning than subordinates, but that dominant females did not, in contrast to our results. These differences in the same population of vervets may reflect differences in the same groups over time or differences in methodology. In their study, scanning included not only gazing into the distance but also looking up and looking down.

Rank and sex differences in moving. To the extent that dominance hierarchies in vervets are related to differential access to high-quality food resources, one might expect subordinate individuals to spend more time moving than dominant individuals because they are denied access to such foods. In fact, such a pattern existed among

females, but not among males. Among males, dominants spent more time moving than subordinates, producing a significant interaction effect between rank and sex (Fig. 7). One possible explanation for this is that dominance among males is not only related to differential access to foods but also to differential access to females and is actively enforced by dominant males in non-feeding situations, resulting in their greater movement. This would imply that high rank is energetically advantageous to females but energetically disadvantageous to males.

Social rank and grooming. High-ranking individuals perhaps stand to gain more than low-ranking individuals from living in groups because they not only benefit from the vigilance of others but are less constrained in their ability to gain food resources and alliance partners (Seyfarth 1980; Cheney 1983; Vehrencamp 1983). Dominant individuals might be expected, therefore, to groom more than subordinates in order to maintain alliances or ease tension (Seyfarth 1980; see below). Increased effort by dominants to maintain access to valued resources could explain the observed patterns of greater allo-grooming of dominants in the larger groups, B and C (significant 'Group \times Rank' interaction, Table 2). On the other hand, there is little evidence from activity patterns that larger groups experienced greater intragroup competition than smaller groups (see below).

Effects of group size on activities

The interpretation of group size effects is hindered by confounding factors. Variation in group size among groups was related to habitat; the two groups (B and C) that lived in *A. xanthophloea* habitat were larger on average than the four groups (A, 2, 3, and 4) that lived in *A. tortilis* habitat (Fig. 1). Variation in group size within groups through time was associated with an ongoing decline in population size (Cheney et al. 1988), shifts in home ranges (Isbell et al. 1990), a period of increased predation (Isbell 1990), and group fusions (Isbell et al. 1991). Confounding factors are probably present in all cases of natural variation in group size, although they may not always be explicitly recognized. However, the fact that significant group size effects were consistent both within and among groups (as for scanning, allo-grooming and 'other' in Table 4) increases the likelihood that group size itself significantly affected activity budgets.

Group size, feeding and moving. If competition for food were greater in larger groups, one might expect that the times spent feeding or moving would be positively correlated with group size (van Schaik et al. 1983; de Ruiter 1986; Janson 1988). However, although larger groups tended to spend more time feeding, this was not statistically significant in either within-group analysis, where habitat type was consistent, or among-group analysis, where habitat type differed (Table 4). Among groups, there was a significant positive relationship between

group size and time spent moving, but this was not supported by the within-group analysis, and may have been due to confounding habitat factors.

Group size and grooming. Not surprisingly, most of the allo-grooming was done by females. Greater allo-grooming among females in groups is a typical pattern in cercopithecine primates, in which females form the stable core of the group (Seyfarth 1980). Female-female relationships in these species involve a complex interplay of kinship, cooperation, and competition (Walters and Seyfarth 1987). It has been suggested that allo-grooming is prevalent in these species because it helps to maintain alliances or ease tension as a result of competition within groups (Seyfarth 1980; Keverne et al. 1989; Cheney 1992), which presumably increases with group size (Alexander 1974; Wrangham 1980; van Schaik 1983). Dunbar (1991) recently reported that allo-grooming increases with mean group size but not body size across catarrhine primate species. He suggested that this supports the hypothesis that allo-grooming functions as a social tool in addition to maintaining hygiene in these species. Because larger groups face greater intragroup competition, females in larger groups may be required to spend more time than individuals in smaller groups in strengthening alliances or reducing tension.

An alternative explanation for increased allo-grooming in larger groups is that ectoparasite loads increase with group size (Dunbar 1991). Dunbar suggested that this can be tested by comparing whether self-grooming, which is not a social activity, increases with group size. This reasoning is complicated by the possibility that self-grooming is a displacement activity that may increase as tension increases in larger groups. Nonetheless, we examined Dunbar's hypothesis by comparing 'other' activities with group size. We were able to separate self-grooming from 'other' activities during sampling from June 1986 until February 1987. Self-grooming constituted 74% of the records for 'other' activities during the non-suckling months (vs. 55% during suckling months). 'Other' activities in non-suckling months, mostly self-grooming, also increased with group size (Table 4). This suggests that the hypothesis that increased allo-grooming functions to maintain hygiene in response to greater ectoparasite loads in larger groups cannot be rejected based on patterns of self-grooming. Future studies of the ecological influences on grooming should help to clarify the relationship between group size and grooming.

Group size and scanning. In vervets, increased allo-grooming and 'other' behavior (when suckling months were excluded) was associated with decreased scanning per individual in larger groups. Unfortunately, it is not possible at this point to determine whether increased allo-grooming in larger groups prevented individuals from scanning more often or whether reduced scanning in larger groups allowed individuals to spend more time allo-grooming. Nonetheless, time spent scanning per individual was negatively correlated with group size whether group size was measured across groups or with-

in groups over time. Individuals in larger groups spent significantly less time scanning than individuals in smaller groups. However, this was more than offset at the group level by the greater expectation that individuals derive greater anti-predator benefits by living in larger groups: group vigilance is maintained or increases while the time cost of vigilance to individuals decreases in larger groups (Pulliam 1973; Powell 1974; Bertram 1980; Barnard 1980).

Although it was not possible to distinguish clearly between scanning for predators and scanning for conspecifics, these results suggest that scanning is not directed primarily toward other monkeys in the same group (see Caine and Marra 1988). If scanning served mainly to monitor the movements and actions of conspecifics within groups, scanning time per individual might be expected to increase rather than decrease in larger groups.

To conclude, changes in activity budgets with group size suggest that vervets derive benefits by living in larger groups. Evidence for costs of living in larger groups was not as strong. Vervets are aggressive between groups and have clearly defined dominance hierarchies within groups. These are expressions of contest competition (van Schaik 1989; Isbell 1991) and their existence suggests that vervets face competition both between and within groups. The relative weakness of the evidence for costs of living in groups derived from activity budgets may be an artifact of a population in decline. At the time of the study, the population declined dramatically as a result of increased predation (Isbell 1990). This may have taken the population well below carrying capacity and may have made the competitive aspects of group-living as reflected in activity budgets more difficult to detect.

Acknowledgements. LAI would like to thank the Office of the President, Kenya, for granting permission to conduct research in Amboseli, J. Else for his assistance in obtaining permission, the Institute of Primate Research for local sponsorship during the fieldwork, D. Cheney and R. Seyfarth for providing the opportunity to study the vervets in Amboseli and B. Musyoka for assistance in the field. The field study was supported by grants from NSF and NIH to D. Cheney and R. Seyfarth, and a Sigma Xi grant-in-aid and a University of California Regents' Fellowship in Animal Behavior to LAI. LAI was supported by the Departments of Anthropology and Zoology, and TPY was supported by the Center for Population Biology and the Department of Botany, at the University of California at Davis. R. Azari offered statistical advice, and A. Harcourt, M. Hauser, and two anonymous reviewers kindly offered constructive criticism of earlier versions of this manuscript.

References

- Alexander RD (1974) The evolution of social behavior. *Annu Rev Ecol Syst* 5:325–383
- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–265
- Barnard CJ (1980) Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). *Anim Behav* 28:295–309
- Bertram BCR (1980) Vigilance and group size in ostriches. *Anim Behav* 28:278–286
- Baldellou M, Henzi SP (1992) Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. *Anim Behav* 43:451–461
- Caine NG, Marra SI (1988) Vigilance and social organization in two species of primates. *Anim Behav* 36:897–904
- Cheney DL (1983) Extra-familial alliances among free-ranging vervet monkeys. In Hinde RA (ed) *Primate social relationships: an integrated approach*. Blackwell Scientific Publications, Oxford, pp 278–286
- Cheney DL (1992) Intragroup cohesion and intergroup hostility: the relation between grooming distributions and intergroup hostility: the relation between grooming distributions and intergroup competition among female primates. *Behav Ecol* 4:334–345
- Cheney DL, Seyfarth RM (1981) Selective forces affecting the predator alarm calls of vervet monkeys. *Behaviour* 76:25–61
- Cheney DL, Seyfarth RM (1985) Vervet monkey alarm calls: manipulation through shared information? *Behaviour* 94:150–166
- Cheney DL, Seyfarth RM (1987) The influence of intergroup competition on the survival and reproduction of female vervet monkeys. *Behav Ecol Sociobiol* 21:375–386
- Cheney DL, Seyfarth RM, Andelman SJ, Lee PC (1988) Reproductive success in vervet monkeys. In: Clutton-Brock TH (ed) *Reproductive success*. University of Chicago Press, Chicago, pp 384–402
- Clutton-Brock TH, Harvey P (1977) Primate ecology and social organization. *J Zool London* 183:1–39
- Dunbar RIM (1991) Functional significance of social grooming in primates. *Folia Primatol* 57:121–131
- Harcourt AH, Stewart KJ (1984) Gorillas' time feeding: aspects of methodology, body size, competition and diet. *Afr J Ecol* 22:207–215
- Harrison MJS (1983) age and sex differences in the diet and feeding strategies of the green monkey (*Cercopithecus sabaues*). *Anim Behav* 31:969–977
- Hoogland JL (1979) The effect of colony size on individual alertness of prairie dogs (Sciuridae: *Cynomys* spp.). *Anim Behav* 27:394–407
- Isbell LA (1990) Sudden short-term increase in mortality of vervet monkeys (*Cercopithecus aethiops*) due to leopard predation in Amboseli National Park, Kenya. *Am J Primatol* 40:41–52
- Isbell LA (1991) Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behav Ecol* 2:143–155
- Isbell LA, Cheney DL, Seyfarth RM (1990) Costs and benefits of home range shifts among vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. *Behav Ecol Sociobiol* 27:351–358
- Isbell LA, Cheney DL, Seyfarth RM (1991) Group fusions and minimum group sizes in vervet monkeys (*Cercopithecus aethiops*). *Am J Primatol* 25:57–65
- Janson CH (1988) Food competition in brown capuchins (*Cebus apella*): quantitative effects of group size and tree productivity. *Behaviour* 105:53–76
- Kavanagh M (1978) The diet and feeding behavior of *Cercopithecus aethiops tanzalus*. *Folia Primatol* 30:30–63
- Kavanagh M (1981) Variable territoriality among tanzalus monkeys in Cameroon. *Folia Primatol* 36:76–98
- Keverne EB, Martensz ND, Tuite B (1989) Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology* 14:155–161
- Lee PC (1983) Ecological influences on relationships and social structure. In: Hinde RA (ed) *Primate social relationships*. Blackwell Scientific Publications, Oxford, pp 225–229
- Marsh C (1981) Time budget of Tana River red colobus. *Folia Primatol* 35:30–50
- Milton K (1980) The foraging strategy of howler monkeys: a study in primate economics. Columbia University Press, New York

- Post D (1981) Activity patterns of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya. *Anim Behav* 29:357–374
- Powell GVN (1974) Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim Behav* 22:501–505
- Pulliam R (1973) On the advantages of flocking. *J Theor Biol* 38:419–422
- Richard A (1977) The feeding behaviour of *Propithecus verreauxi*. In Clutton-Brock TH (ed) *Primate ecology: studies of feeding and ranging behavior in lemurs, monkeys, and apes*. Academic Press, New York, pp 72–96
- Robinson J (1988) Group size in wedge-capped capuchin monkeys *Cebus olivaceus* and the reproductive success of males and females. *Behav Ecol Sociobiol* 23:187–197
- Ruiter J de (1986) The influence of group size on predator scanning and foraging behaviour of wedge-capped capuchin monkeys (*Cebus olivaceus*). *Behaviour* 98:240–258
- Schaik CP van (1983) Why are diurnal primates living in groups? *Behaviour* 87:120–143
- Schaik CP van (1989) The ecology of social relationships amongst female primates. In: Standen V, Foley RA (eds) *Comparative socioecology: the behavioural ecology of humans and other mammals*. Blackwell Scientific Publications, Oxford, pp 195–218
- Schaik CP van, Noordwijk MA van, DeBoer RJ, Den Tonkelaar I (1983) The effect of group size on time budgets and social behaviour in wild long-tailed macaques. *Behav Ecol Sociobiol* 13:173–181
- Seyfarth RM (1980) The distribution of grooming and related behaviours among adult female vervet monkeys. *Anim Behav* 28:798–813
- Seyfarth RM, Cheney DL, Marler P (1980) Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Anim Behav* 28:1070–1094
- Sokal RR, Rohlf FJ (1981) *Biometry*. WH Freeman, New York
- Stanford CB (1991) The capped langur in Bangladesh: behavioral ecology and reproductive tactics (*Contr Primatol* vol 26). Karger, New York
- Struhsaker TT (1967) Ecology of vervet monkeys in the Masai-Amboseli Game Reserve, Kenya. *Ecology* 48:891–904
- Struhsaker TT (1973) A recensus of vervet monkeys in the Masai-Amboseli Game Reserve, Kenya. *Ecology* 54:930–932
- Struhsaker TT (1975) The red colobus monkey. University of Chicago Press, Chicago
- Struhsaker TT (1976) A further decline in numbers of Amboseli vervet monkeys. *Biotropica* 8:211–214
- Sussman RW (1977) Feeding behaviour of *Lemur catta* and *Lemur fulvus*. In: Clutton-Brock TH (ed) *Primate ecology: studies of feeding and ranging behavior in lemurs, monkeys, and apes*. Academic Press, New York, pp 1–36
- Terborgh J (1983) *Five new world primates: a study in comparative ecology*. Princeton University Press, Princeton, New Jersey
- Vehrencamp SL (1983) A model for the evolution of despotic vs. egalitarian societies. *Anim Behav* 31:667–682
- Walters JR, Seyfarth RM (1987) Conflict and cooperation. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 306–317
- Waser PM (1977) Feeding, ranging and group size in the mangabey (*Cercocebus albigena*). In: Clutton-Brock (ed) *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes*. Academic Press, New York, pp 182–222
- Watts D (1988) Environmental influences on mountain gorilla time budgets. *Am J Primatol* 15:195–211
- Western D (1983) *A wildlife guide and a natural history of Amboseli*. General Printers, Nairobi
- Western D, Praet C van (1973) Cyclical changes in the habitat and climate of an East African ecosystem. *Nature* 241:104–106
- Whitten P (1983) Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *Am J Primatol* 5:139–159
- Wolf FM (1986) *Meta-analysis (Quantitative applications in the social sciences no. 59)*. Sage Publications, Beverly Hills, California
- Wolfheim J (1983) *Primates of the world: distribution, abundance, and conservation*. University of Washington Press, Seattle, Washington
- Wrangham RW (1980) An ecological model of female-bonded primate groups. *Behaviour* 75:262–300
- Wrangham RW (1981) Drinking competition in vervet monkeys. *Anim Behav* 29:904–910
- Young TP, Lindsay WK (1988) Role of even-age population structure in the disappearance of *Acacia xanthophloea* woodlands. *Afr J Ecol* 26:69–72