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Group size and foraging efficiency in yellow baboons

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Summary. I studied the foraging behaviour of adults in three different-sized groups of yellow baboons (*Papio cynocephalus*) at Amboseli National Park in Kenya to assess the relationship between group size and foraging efficiency in this species. Study groups ranged in size from 8 to 44 members; within each group, I collected feeding data for the dominant adult male, the highest ranking pregnant female, and the highest ranking female with a young infant. There were no significant differences between groups during the study in either the mean estimated energy value of the food ingested per day for each individual ($385 \pm 27 \text{ kJ kg}^{-1} \text{ day}^{-1}$) or in the estimated energy expended to obtain that food ($114 \pm 3 \text{ kJ kg}^{-1} \text{ day}^{-1}$). Mean foraging efficiency ratios, which reflect net energy gain per unit of foraging time, also did not vary as a function of the size of the group in which the baboons were living. There was substantial variation between days in the efficiency ratios of all animals; this was the result of large differences in energy intake rather than in the energy expended during foraging itself. The members of the smallest group spent on the average only one-half as much time feeding each day as did individuals in the two larger groups. However, they obtained almost as much energy while foraging, primarily because their rate of food intake while actually eating tended to be higher than the rate in the other groups. The baboons in the small group were observed closer to trees that they could climb to escape ground predators, and they also were more likely to sit in locations elevated above the ground while resting. Such differences would be expected if the members of the small group were less able to detect approaching predators than individuals that lived in the larger groups. The results of this study suggest that predator detection or avoidance, rather than increased foraging efficiency, may be the primary benefit of living in larger groups in this population.

Introduction

The potential advantages of foraging in groups, and the relationships between average group size within a population and resource distribution and abundance, have been the subjects of considerable interest and speculation (see recent reviews by Bertram 1978; van Schaik 1983; Pulliam and Caraco 1984). The hypothesized benefits of feeding in groups include increased nutrient or energy intake resulting from information sharing among group members about the quality or location of food patches, defense of resources from conspecifics, or increased predator detection or cooperative defense against predators. The potential costs of group foraging include increased competition for scarce resources, either through actual displacements from contested resources during dominance interactions, or through resource depression resulting from many animals feeding in the same area at the same time (Alexander 1974). For any population, available resources may either set an upper limit for group size, or alternatively, costs and benefits may vary as a function of the number of individuals feeding together such that there is some optimum group size for which foraging efficiency is maximized.

Studies of flocking in birds and mammals have shown that individuals may benefit from feeding in groups through a reduction of per capita time devoted to searching for predators (vigilance), and a resultant increase in time that is available for foraging (e.g. Powell 1974; Berger 1978; Caraco 1979; Lazarus 1979; Sullivan 1984). Such benefits appear to arise primarily in species where the behaviours involved in feeding are physically incompatible with those used to scan for predators (e.g., pecking for seeds or grazing). An assumption common to these studies is that individual feeding time is related directly to the amount or quality

of food ingested; whether or not this will always be the case is unknown (see also below). In addition to effects on vigilance, several laboratory studies have provided evidence that group foraging may increase the rate at which food patches are located in the environment, thereby reducing the per capita time spent searching for food (Krebs et al. 1972; Pitcher et al. 1982; see also Pulliam and Millikan 1982). This would not only increase time available for feeding, but also reduce the total energetic costs of foraging itself.

The purpose of this study was to examine the individual costs and benefits of foraging in three different-sized groups of yellow baboons. The possible importance of group foraging in the evolution of primate social organization has been the subject of extensive discussion (e.g. Crook 1970; Jolly 1972; S.A. Altmann 1974; Clutton-Brock and Harvey 1977; Wrangham 1980; Terborgh 1983; van Schaik 1983). Despite this interest, there have been few attempts to quantitatively compare feeding rates or foraging efficiencies of members of groups of different sizes in free-living populations (Rowell 1979). Most previous studies have examined the relationship between group size and various components of individual time budgets (e.g. average time spent feeding: van Schaik et al. 1983) or movement patterns (e.g., Waser 1977); however, as with the studies mentioned above, it is usually unknown whether or not these variables directly reflect levels of foraging efficiency itself. The yellow baboon is an excellent subject for studies of foraging ecology. This species has been studied extensively at Amboseli National Park, Kenya since 1963 (e.g. Altmann and Altmann 1970; J. Altmann 1980; S.A. Altmann 1974, 1979; Hausfater 1975; Post 1981; Post et al. 1980). Groups do not defend territories that might differ in vegetative quality, but often forage at different times in the exact same areas. Most feeding occurs in relatively open areas on or near the ground, and the groups involved in this study were habituated to the presence of human observers. The baboons could therefore be observed from distances of three to five meters without disturbance, and this enabled me to collect not only time-budget data, but also to estimate the amount and type of food actually ingested by the study animal. In addition, data on the nutrient composition of most of the foods eaten by baboons at Amboseli are available (S.A. Altmann et al., in press). The specific aims of this research were therefore to (1) estimate the amount and energy value of the food obtained during the day for three matched individuals living in each group, as well as the energy expended by those

individuals during foraging and throughout the day, (2) test the hypothesis that there is a relationship between group size and foraging efficiency, defined as net energy gain per unit of foraging time, in this population, and (3) examine other aspects of the behaviour of the three groups that might be related to predator detection or avoidance.

Methods

Study area and sampling methods. This study was done from October 1979 through February 1980 at Amboseli National Park, Kenya. The Amboseli basin contains large areas of open grasslands (primarily *Sporobolus* and *Cyperus* spp.), *Acacia tortilis* savannah, and patches of fever tree (*A. xanthophloea*) woodlands surrounding waterholes and swamps (see Western and van Praet 1973). I studied three adult individuals in each of three different groups of baboons: Limp's Group (8 members, 3 adults), Hook's Group (31 members, 12 adults), and Alto's Group (44 members, 17 adults). These groups had overlapping home ranges, and included both the smallest and largest groups living in the western portion of the park (median group size of the five groups present in this area in 1979 was 27). The smallest group, Limp's, contained three adults: a single male, a female that appeared to be pregnant at the start of the study, and a lactating female with a one-month-old infant. Previous research on baboons at Amboseli (Post et al. 1980) has shown that the age, sex, reproductive condition and dominance status of an individual within its group can affect its foraging behaviour. In order to control for these variables, each adult in Limp's Group was matched for sampling purposes with a similar individual in the remaining two groups: specifically, the highest ranking adult male, the highest ranking female that was pregnant at the start of the study, and the highest ranking female with an infant that was less than six months old (Table 1).

Twenty-minute focal animal samples (J. Altmann 1974) were taken each hour between 0700 and 1800 hours on one individual per day. Each sample began at 20 min after the hour, or at exactly one minute intervals thereafter for 10 min; if the sample had not begun at that point it was cancelled until the next scheduled hourly period. The three focal animals in one group were observed on consecutive days; after one day for data analysis, I rotated samples to the next group to minimize seasonal differences in available food. Days during which I was unable to obtain six or more samples due to equipment failure, etc., were excluded from subsequent analysis. Total contact time with the baboons during this study was 844 hours; non-feeding observation time was devoted to recording movement patterns, dominance and reproductive interactions, and to identifying and collecting plants. Sufficient feeding samples were obtained for each focal animal on five to seven separate days (1003–1370 total sample minutes); this resulted in 18–19 sample days for each group.

During each focal sample I made a continuous record of the elapsed time of each activity bout (feeding, moving, socializing, resting, or drinking), as well as intervals when the animal was "out of sight", defined as periods when I could not accurately determine whether the animal was feeding or performing some other activity. Activity categories were exhaustive and mutually exclusive. Feeding bouts began when the animal first made physical contact with a food item (except when used as

Table 1. Description of yellow baboon groups and focal animals observed at Amboseli National Park, Kenya

Group	Group size	Size change (10/79–2/80)	Focal animals	Sex	Rank within sex	Reproductive status		Focal minutes
						Start	Finish	
Limp's	8 (3) ^a	0	Caesar	♂	1	–	–	1,003
			Lily	♀	1	Pregnant (?)	–	1,056
			Maggie	♀	2	Inf. (10/79) ^b	–	1,085
Hook's	31 (12)	+1	Harvey	♂	1	–	–	1,370
			Pindua	♀	1	Pregnant	Inf. (12/79)	1,083
			Kupita	♀	2	Inf. (8/79)	–	1,320
Alto's	44 (17)	+2	Teta	♂	1	–	–	1,234
			Striper	♀	5	Pregnant	Inf. (12/79)	1,053
			Spot	♀	1	Inf. (9/79)	–	1,060
Total								10,264

^a Total group size at start of study, with number of adults in parentheses

^b Date (month/year) of birth of infant

a substrate for locomotion), and ended when the baboon either did not contact a new item of the same food type for at least two seconds, switched to a new food type, or began a different activity. I recorded the species name and part of the plant or animal eaten during each bout, and whenever possible, the number of individual items (berries, leaves, etc.) ingested during that bout. Socializing was defined as any interactive behaviour between two or more baboons, including grooming and agonistic behaviour (each recorded separately in the field). Moving and drinking are self-explanatory. I also took point (instantaneous) samples (J. Altmann 1974) 30 s before and after each focal sample, during which I recorded the distance from the focal animal to the nearest tree over 10 m in height. The location of the center of the study group was plotted at 30-min intervals throughout the day on aerial photographs of the study area; these maps were then used to determine home range sizes and overlap. Behavioural data were collected using a MORE electronic event recorder (Observational Systems, Seattle, Washington, USA) and stored on cassette recording tapes.

Estimation of daily food and energy intake. I calculated two time budgets: a general activity time budget, in which all feeding observations were collapsed into a single category, and a food specific time budget where each food type was treated separately. Each time budget combined the data from all 20-min focal samples taken on one day into the relative proportion of total in-sight sample time that the individual performed each activity or consumed a particular food type on that day. Alternative methods of constructing time activity budgets and estimating nutrient intake are discussed in detail by S. Altmann (in press).

The energy content of the food obtained by a baboon during one sample day was estimated by

$$\text{Intake (kJ/day)} = \sum_i P_i \cdot S \cdot B_i \cdot C_i \cdot D_i \quad (1)$$

where P_i is the proportion of total sample time (in-sight) on a particular day that the focal animal spent feeding on food type i , S is the number of seconds in the 24-h period during which the baboons are usually active and potentially foraging (39,600 s, or 11 h), B_i is the mean number of items of food i consumed by the individual per second (items/s), C_i is the average dry weight (0% moisture content) of an item of food i (g/item) and D_i is the estimated energy content per gram dry weight of food i (kJ/g).

The first four factors in equation (1) estimate the total dry weight of the food obtained during a sample day; the inclusion of D_i then converts this to estimated energy intake. B_i was determined by counting whenever possible the number of items placed into mouth and the total length in seconds of each feeding bout for all food types for each focal animal during the field samples; a total of 2,409 different bouts involving from one to 203 items per bout were measured during the study. Values of C_i and D_i were determined for most foods from the results of standard proximate analyses (e.g., Crampton and Harris 1979) of representative samples of food items collected previously at Amboseli by S.A. Altmann, D. Klein, D. Post and others (S.A. Altmann et al., in press). Whenever possible, I used data from samples of the same maturity stage and that had been obtained during the same season of the year as this study to control for any seasonal variation in the nutrient content of each food type. A total of 35 different plant species and five animal species was eaten by the members of the three groups; these were further divided into 56 different food categories depending upon the part of the plant consumed or its developmental stage. For example, the grass *Sporobolus ioclados* was subdivided into blades, blade bases, and corms. Whenever I was unable to determine the species identity of a particular food, the observation was placed into a different category depending upon the amount of information available (e.g., unidentified grass corm, unidentified plant, unidentified food, etc.); this created 8 additional categories, for a total of 64 different possible feeding activities.

Specific compositional data from proximate analyses were available for 39 of the 64 different food categories; these items comprised 86% of the total observed feeding time of all focal animals. Values for 8 additional foods were estimated from analyses of taxonomically related species that had been collected at Amboseli (10% of total feeding time), and from published data on similar species for 9 categories (1% of feeding time). For feeding bouts where I was unable to identify the specific food type (3% of feeding time), I used averaged values for that food class from the samples collected at Amboseli.

The results of the proximate analyses (percentage composition of moisture, ash, crude protein, ether extractives (primarily lipids), fiber, and soluble carbohydrates or N.F.E.) were used to calculate the average dry weight of an item with zero moisture content of food type i by multiplying one minus the water content times the mean weight of the items during proximate

analysis. I then calculated the Physiological Fuel Value (PFV), per gram dry weight, of each food. The species eaten by the baboons during this study, and their estimated energy content per gram, are given in Stacey (MS). Physiological Fuel Values are used in this report, rather than gross energy content, because they estimate the actual amount of energy which can be assimilated from a particular food (see Crampton and Harris 1979). Analysis using gross energy content did not affect any of the conclusions presented here. Since the PFV of natural foods for baboons are presently unknown, I used values obtained from human studies as the best estimates currently possible (Leung 1968; Stacey MS). Grass blades, an important part of the baboons' diet, are not normally eaten by humans, and no estimate of the PFV of this food exists. A major component of grass blades is fiber. Knapka and Morin (1979) found that captive baboons would digest between 38% and 47% of the fiber in several laboratory diets. Since the source of fiber in their study was primarily wheat bran, their estimate is probably too high for the digestibility of fiber in grass blades. I therefore used a lower value of 20% digestibility of fiber in the calculation of the PFV of grass blades.

All intake values were converted to a per kilogram of body mass basis during statistical analysis in order to compare individuals of different body sizes. The focal animals in this study were not weighed in the field. I instead used the data of Bramblett (1969), as modified by J. Altmann (1980) to estimate the mass of the adult males as 22.5 kg and adult females as 11 kg. The female Lily in Limp's group was noticeably larger than any other female studied; I estimated her mass to be 12.5 kg, which is within the range of adult females collected by Bramblett (1969).

Estimation of daily energy expenditures. The amount of energy expended by an individual during a sample day was estimated from the following equation (see also Coelho et al. 1976):

$$\text{kJ/day (Expenditure)} = \sum_a P_a \cdot D \cdot E_a \quad (2)$$

where P_a is the proportion of total sample time (in-sight) on that day that the animal spent performing activity a , D is the number of seconds in the 24-h day and night period, and E_a is the estimated energetic cost of activity a in kJ/s.

For this analysis, the 24-h period was divided into two parts: (1) "daytime" (11 h - see above) where the activity time budgets were used to directly estimate energy expenditure, and (2) "nighttime", when the animals are either sleeping or resting in trees (13 h), and where energy expenditure was assumed to be equal to the basal metabolic rate (Kleiber 1961):

$$\text{BMR} = 70 W^{0.75} \text{ kcal/day}$$

or $0.0034 \text{ kJ}/W^{0.75}/\text{s}$, where W is the body mass of the individual (kg). This estimate does not include any costs of thermoregulation during the night.

All behaviours recorded during the focal samples were placed into one of 6 different activity categories: feeding, moving, resting, grooming, agonistic interactions, and "other social" behaviours. The cost of each activity was taken from the estimates made by Coelho and Bramblett (MS) for various baboon behaviours, and varied according to the body weight of the animal. Resting was given an energetic cost of $0.00488 \text{ kJ}/\text{kg}^{0.75}/\text{s}$; grooming, "other social" behaviours and feeding, $0.00839 \text{ kJ}/\text{kg}^{0.75}/\text{s}$; and agonistic behaviour, $0.03695 \text{ kJ}/\text{kg}^{0.75}/\text{s}$. The energetic cost of moving was calculated for each animal from the equation of Tucker (1970) for quadrupedal mammals:

$$L(\text{kcal kg}^{-1} \text{km}^{-1}) = 0.100 (10)^E$$

where

$$E = 1.67 W^{-0.126}.$$

After conversion of L to kilojoules, the average cost per second of moving was determined for each animal from

$$\text{kJ/s} = L \cdot W \cdot V$$

where V is the average velocity of the individual while moving (km/s). Values of V were obtained from the average of at least five different field measurements of total distance traveled (measured with a meter tape) and elapsed time to move that distance for each focal animal. Values of V ranged from 0.68 ms^{-1} (2.45 km per hour) for the female Striper in Alto's Group to 0.98 ms^{-1} (3.53 km per hour) for the adult male Caesar in Limp's Group.

The estimates of daily energy expenditures presented in this paper do not include any energy costs associated with growth, thermoregulation, or reproduction. I was not able to measure expenditures due to the first two factors, but the animals I studied were all adults and presumably growing very little. I attempted to control for reproductive expenditures by matching focal animals across groups by sex and reproductive status.

Analysis. Equations 1 and 2 were used to estimate the energy intake and energy expenditures of the focal animal on each sample day. I then calculated a net foraging efficiency value for each day, defined as: $(b-c)/T$, where b is the total energy intake from ingested food, c is the energy expended to obtain that food, and T is the amount of time spent during foraging. Foraging has two components: the amount of time or energy expended while actually handling and ingesting feed, and the time or energy used to move within and between different food patches. Baboons are highly opportunistic foragers, and they may feed at any time and anywhere along the route that they travel each day (including in or below their sleeping trees). Under these conditions, specific movement patterns or travel times cannot be assigned to individual food patches. I therefore considered all energy expended in the activity category of moving to be part of the total cost of foraging each day.

The significance of differences between groups for each variable measured in this study was determined using the SAS Generalized Linear Model Procedure (SAS 1979). The statistical model employed was Group ($n=3$) by Focal Animal ($n=3$), with animals nested within groups and sample days as a repeated measure (n is variable). F ratios for the group main effect were calculated using the animal-within-group mean square as the error term (see Keppel 1973). Statistical procedures used for other comparisons are described in the results section; two-tailed tests of significance were used in all cases.

The methods used here to estimate energy intake and expenditures involve several simplifications that could potentially affect statistical comparisons between groups. First, in Eqs. 1 and 2, I used constants for all factors except the time-budget information (P_i or P_a). In actuality, of course, each factor is a random variable, and each has an associated variance term. The net effect of these terms is to increase the standard error of the estimates of mean energy intake and expenditure (Travis 1982). I have no information on the variance of any of the factors; however, any systematic bias resulting should be reduced by the fact that I used the same constants for all animals, except B_i , which varied between animals. The sampling errors of the remaining terms are probably similar across groups. Secondly, to calculate the time-budget of an animal on a particular day, I have included only those periods during the sample when the baboon was "in sight". This procedure,

which is commonly employed in time-budget studies, may underestimate the relative contribution to the diet of some foods, if an individual is more likely to go "out of sight" when feeding on that species in comparison to others (see Altmann, in press). However, the inclusion of activity bouts that are "censored" by the animal going out of sight will affect comparisons between groups only if individuals in one group are more likely to go out of sight per unit time when feeding on a particular food than are members of another group when feeding on the same food, rather than while consuming different foods. Analysis of several food categories indicates that there were not significant differences between groups in this respect.

A second factor that affects the probability that a focal animal will go out of sight during samples is the degree to which members of the group are habituated to the presence of human observers. I did not begin actual behaviour sampling until the focal animals could be observed from distances of 10 m or less without noticeably affecting their behaviour. To further check whether or not the behaviour of the baboons changed as a function of the amount of time they had been observed, correlation coefficients (Zar 1974) were calculated between the cumulative number of days that the group had been studied and the percent time the focal animal spent feeding, moving, resting, socializing, or was out of sight. There were no significant correlations ($P < 0.05$) between cumulative sample days and any variable in either the small or medium sized groups. The sole significant relationship in the large group (Alto's) was with the percentage of time spent socializing ($r = 0.524$, $P < 0.05$); this result may have occurred by chance alone. These results show that the behaviour of the animals did not systematically change over the course of the study as they became more habituated to human observers. Since cumulative sample days also reflect elapsed time from the beginning of the study, the absence of significant correlations indicate there were no systematic changes in the behaviour of individuals that might be the result of seasonal changes in the environment.

Results

Home ranges

Home range size between October 1979 and February 1980 varied with group size: the smallest group occupied the smallest range (Limp's, 12.6 km²), Hook's utilized 15.9 km², and the largest group had the largest range (Alto's, 19.6 km²). The groups did not defend specific areas of their ranges from other baboons: when two groups approached each other, one of them (usually, but not always, the smaller group) typically either moved off in a different direction or waited until the other group left the area (see also Altmann and Altmann 1970). The portion of each group's home range that overlapped with the range of at least one other study group was roughly similar, and included between 22% and 27% of the total area utilized by each group. The use of overlap areas during foraging was high: Limp's Group fed in this portion of its home range on 64% of the days during which it was observed, Hook's Group on 62% and Alto's Group on 100% of sample days. Census and mapping records taken as part of the long term project

at Amboseli indicate that, over longer time periods, both total home range size and the amount of overlap between these three groups are considerably greater than that recorded during the period of this study. Thus, when foraging in areas of overlap, each group had access to the same resources as the other group(s).

Time-activity budgets

The mean daily proportion of time that the three focal animals in each group spent feeding, moving, resting and socializing is given in Fig. 1. Drinking involved less than 1% of total sample time in all groups, and was dropped from subsequent analyses. In comparing time-budgets, only three of the four activity categories are statistically independent, since total time must sum to 100%. There were significant differences between groups only in the proportion of time spent feeding ($F = 16.98$, $P < 0.05$, with arcsine transformation of proportions: Zar 1974), although differences in resting time approached statistical significance ($F = 4.09$, $P = 0.07$). The time budgets of members of the medium and large groups were essentially the same. Individuals in the small group, however, spent only one-half as much time feeding during the day as those in the two larger groups ($\bar{x} = 21\%$ vs 41% in both Hook's and Alto's groups; $P < 0.05$, Duncan's multiple range test after ANOVA). Surprisingly, the time devoted to social behaviour was approximately the same in all groups, and therefore did not increase with the number of potentially interacting partners present within a group.

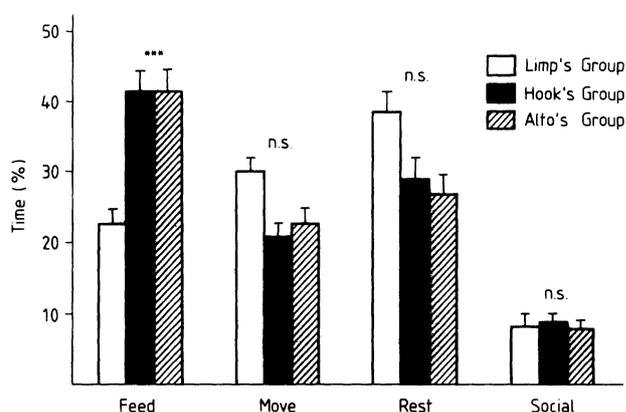


Fig. 1. Activity time budgets of members of three different-sized groups of yellow baboons (Limp's Group: 8 members, 3 adults; Hook's Group: 31 members, 12 adults; Alto's Group: 44 members, 17 adults). Values are the mean and standard errors of the daily proportion of time spent performing each activity. *** indicates significant differences between groups where $P < 0.005$; n.s. indicates not significant ($P > 0.05$)

The time budgets of the focal animals within a group were very similar: of 36 possible comparisons (4 activity categories between 3 individuals in each of 3 groups) only two were significantly different at the $P < 0.05$ level. This number of significant differences would be expected to occur by chance alone ($\chi^2 = 0.53$, $P < 0.05$). These results indicate that each individual within a group spent approximately the same amount of time feeding and performing other activities per day as did the other members of the same group.

Diet composition and overlap between groups

The majority of the diet of each group consisted of plant material; individual species and percentage feeding time for each group are given in Stacey (MS). Consumption of animal food was relatively rare during this study, but it may be nutritionally important (Hausfater 1976). A small number of foods made up the bulk of the diet in each group: the top ten foods ranked in order of relative feeding time involved between 67% and 76% of total time spent feeding in each group. I used as a quantitative measure of diet diversity: $1/\sum P_i^2$, where P_i is the relative percentage contribution to the diet of the i th taxon or food category. This measure combines both the richness and evenness components of taxa abundance patterns in the diet, and can be used to estimate the "niche breadth" of the diet (see Rottenberry 1980). Two measures of diet diversity for each group were calculated: feeding time diversity, where P_i is the relative proportion of time spent feeding on each taxon combined over all samples, and an energy intake diversity, where P_i is the relative contribution in kJ of the i th taxon to total estimated energy intake. Feeding time diversity values were similar for all groups: 13.37 in the small group, 13.93 in the medium group, and 14.14 in the large group. There was greater variation when the diet was considered in terms of the energy content of food eaten: diversity values for the three groups were 8.31, 11.78 and 10.85 respectively. These results indicate that while baboons in each group tended to distribute their foraging time between potential food categories in similar ways, individuals in the smallest group obtained more of their total energy intake from a smaller subset of foods than did members of the two larger groups. The two methods of calculating diet diversity yield different results because the energy intake measure includes variation in both the energy content of each food class as well as rate at which items are obtained per unit of feeding time.

The similarity of the diets of the three baboon groups was measured using the "correlational" index of Stander (1970):

$$\text{SIMI} = \frac{\sum x_i y_i}{\sqrt{\sum x_i^2 \sum y_i^2}}$$

where x_i is the relative contribution of food category i to the diet of one group (either feeding time or energy) and y_i the relative contribution of the same category to the diet of the second group. The diet similarity values of the three groups during the period of this study using percentage feeding time were: 0.476 between Limp's and Hook's Groups, 0.507 between Limp's and Alto's Groups, and 0.588 between Hook's and Alto's Groups. A slightly different pattern emerges when similarity is measured on the basis of energy: these values were, respectively, 0.577, 0.585, and 0.460. The observed overlap in the diets of the three groups during this study by either measure when analyzed at the level of individual species and parts of each plant was surprisingly low. However, if the diets are compared on the basis of general food type (e.g., all grasses, all fruits, all leaves, etc.; see Table 2), the percentage of time spent feeding on each category is almost identical. The similarity values between the groups based on the data in Table 2 are: 0.935 between Limp's and Hook's Groups, 0.990 between Limp's and Alto's Groups, and 0.945 between Hook's and Alto's Groups. These results indicate that although the groups fed upon the same types of foods in very similar proportions during the study, the actual species utilized by each group were frequently different.

Table 2. Percentage of total feeding time spent by members of three groups of yellow baboons consuming various types of food between October 1979 and February 1980. The grass category includes all parts of grass plants eaten by the baboons. The miscellaneous category includes *Chlorophytum* bulbs, mushrooms, unidentified plants and unknown foods

Food type	Percentage of total feeding time			
	Limp's group	Hook's group	Alto's group	All groups
Grasses	38.40	39.79	43.06	41.11
Fruits	33.03	21.94	30.96	27.64
Seeds	11.82	26.83	12.15	18.03
Sap	10.44	7.26	6.65	7.63
Flowers	2.01	1.74	5.74	3.28
Leaves	2.38	0.52	0.71	0.96
Animal matter	0.12	1.76	0.13	0.82
Miscellaneous	1.79	0.13	0.63	0.79

Table 3. Estimated daily food (g dry mass kg⁻¹day⁻¹) and energy (kJ kg⁻¹day⁻¹) intake ($\bar{X} \pm \text{SE}$) of members of three different-sized groups of yellow baboons. The number in parentheses after the group name is the total number of sample days, with three focal animals in each group. *F*-ratios for the group main effects were determined using the animal-within-group mean square as the error term (see Methods); *df*=2,6 for all comparisons

Group (<i>n</i>)	Size	Protein	Fats	Carbo- hydrates (NFE)	Crude fiber	Ash	Total	PFV energy content
Limp's (18)	8	4.17 ± 0.44	1.84 ± 0.32	11.58 ± 1.28	4.63 ± 0.66	2.80 ± 0.42	25.03 ± 2.52	345 ± 37
Hook's (19)	31	4.36 ± 0.55	1.40 ± 0.19	15.11 ± 2.03	4.93 ± 0.61	2.56 ± 0.47	28.35 ± 3.44	422 ± 51
Alto's (18)	44	5.39 ± 0.80	1.91 ± 0.35	12.83 ± 1.59	5.45 ± 0.75	3.57 ± 0.64	29.15 ± 3.96	387 ± 51
$\bar{X} \pm \text{SE}$		4.63 ± 0.36	1.71 ± 0.17	13.21 ± 0.97	5.00 ± 0.38	2.97 ± 0.30	27.53 ± 1.92	385 ± 27
<i>F</i>		0.78	2.56	0.33	0.24	1.25	0.28	0.22
<i>P</i>		>0.45	>0.15	>0.70	>0.75	>0.35	>0.75	>0.80

Estimated daily food and energy intake

The data given above show that not only did the members of the three groups spend different amounts of time foraging each day, but also they frequently ate different foods. Were the baboons in each group able to obtain the same total amount of food each day in spite of these differences, and was this food of equal nutritional value? The mean amount of food obtained per day and the total PFV energy intake for the focal animals in each group are given in Table 3. There were no significant differences between groups in the amount of either protein, lipids, fiber or soluble carbohydrates (N.F.E.) obtained per day. The mean total dry weight of food ingested and PFV energy content of that food per individual also did not change with group size.

There was substantial daily variation in food and energy intake among all animals. For example, the estimated total dry weight obtained by the adult male Teta in Alto's Group ranged from 159 to 1,320 g per day. This food contained energy values of 2,462 kJ and 13,757 kJ respectively, more than a five-fold difference. The smallest range observed in any animal was for the female Lily in Limp's Group, with 183–420 g of food and 2,523–5,683 kJ per day. Since individuals in groups may share information about the location or quality of food resources, it has been suggested that group foraging might either reduce variance in daily food intake (e.g., Caraco 1979) or decrease the probability that an animal would be unable to obtain some minimum energy or nutrient requirement necessary for survival (e.g., Thompson et al. 1974). Variance in both daily food intake and energy influx, however, tended to be greater in the larger groups rather than smaller (Table 3): the difference in the variance of the former

measure approached statistical significance between the small and large groups [variance ratio test (Zar 1974): $F=2.44$; $df=17,17$; $0.10 > P > 0.05$]. The reasons why the variance might tend to increase when there are more individuals in a group are unknown.

Although the members of the small group spent on the average only one-half as much time feeding per day as did individuals in the two larger groups (23% vs. 41% in both Hook's and Alto's Groups; Fig. 1), they were able to obtain almost as much food and energy while foraging. Feeding time alone would be a poor predictor of total intake if individuals differ in the rate at which they ingest food items per unit time (commonly termed "bite rate"). Bite rates were measured for a total of 2409 different feeding bouts during the focal animal samples. In order to test the possibility that individuals in the small group ingested food at a higher rate than did those in the other groups, I compared mean bite rates for every food category for which I had obtained at least 10 separate measurements in at least two different groups. Sufficient samples were available for 14 different foods, which involved 57.2% of the feeding time of all groups (the limited number of comparisons that were possible by these criteria were the result in part of the tendency of the groups to feed on different foods during the study; see the discussion of diet overlap above). Pairwise differences in mean bite rates were evaluated using the Student's *t*-test. Of 16 possible comparisons between the small group and either of the two large groups, members of Limp's Group had a significantly higher mean bite rate ($P < 0.05$) in 8 cases, was equal in 8 cases, and significantly lower in none. The distribution of these results is significantly different from those that would be expected to arise by chance alone ($\chi^2 = 13.34$, $P < 0.005$). In contrast, for the 12 pos-

Table 4. Comparison of daily energy expenditures ($\bar{X} \pm \text{SE}$) of members of three different-sized groups of yellow baboons. The number in parentheses is the total number of sample days for all focal animals in the group. Statistical model for between-group comparisons as in Table 3; $df=2,6$ in all cases

Group (<i>n</i>)	Size	Feeding (kJ kg ⁻¹ day ⁻¹)	Moving (kJ kg ⁻¹ day ⁻¹)	Total daytime activities (kJ kg ⁻¹ day ⁻¹)	Total 24-h period (kJ kg ⁻¹ day ⁻¹)
Limp's (18)	8	39 ± 3	72 ± 4	165 ± 3	247 ± 4
Hook's (19)	31	71 ± 5	44 ± 5	162 ± 4	243 ± 4
Alto's (18)	44	72 ± 6	44 ± 4	143 ± 3	225 ± 4
$\bar{X} \pm \text{SE}$		61 ± 3	53 ± 3	157 ± 2	238 ± 3
<i>F</i>		9.40	19.82	5.68	1.56
<i>P</i>		<0.05	<0.005	<0.05	>0.05

sible comparisons involving only the medium and large groups, Hook's was equal to Alto's Group for 7 foods, higher for 4, and lower for 1. These latter results would be expected since feeding time and dietary intake were approximately the same in both groups. This analysis indicates that the members of the small group apparently compensate for their lower total feeding time through a higher rate with which they obtain food while feeding.

Estimated daily energy expenditures

Table 4 gives the estimated mean daily energy expenditures for the focal animals in each group for the activity categories of feeding and moving, for total daytime activities, and for the entire 24-h period. There were significant differences ($P < 0.05$) between groups in each category of energy expenditures except for during the total 24-h period. Specifically, the focal animals in the small group (Limp's) spent significantly less energy per kg of body mass per day feeding, and more energy moving, than did the members of the two larger groups (Duncan's multiple range test after ANOVA, $P < 0.05$). When all other behaviours (i.e., social behaviours and resting) are included for the 11-hour active period, the small group expended a slightly greater amount of energy than the medium sized group, while that for the largest group was significantly lower than either of the two smaller groups. The same trend of decreasing energy expenditures with increasing group size existed when nighttime sleeping or resting costs are included, but the differences between groups were no longer significant.

Foraging efficiencies of individuals in different-sized groups

Foraging efficiency is defined as the energy obtained by an individual from the food it ingests

Table 5. Mean efficiency ratios and daily energy balance ratios ($\pm \text{SE}$) for the members of three different-sized groups of yellow baboons. Feeding efficiency includes only the time and energy spent during feeding; foraging efficiency includes the costs of both feeding and moving during the day (see text). The number in parentheses is the total sample days for each group. Statistical model for between-group comparisons as in Table 3; $df=2,6$ in all cases

Group	Group size	Feeding efficiency (kJ/min)	Foraging efficiency (kJ/min)	Daily energy balance
Limp's (18)	8	28.0 ± 2.4	9.1 ± 1.3	1.38 ± 0.13
Hook's (19)	31	18.5 ± 2.4	10.6 ± 1.7	1.71 ± 0.20
Alto's (18)	44	15.8 ± 2.2	8.6 ± 1.8	1.71 ± 0.23
$\bar{X} \pm \text{SE}$		20.7 ± 1.5	9.4 ± 0.8	1.60 ± 0.11
<i>F</i>		11.22	0.51	0.55
<i>P</i>		<0.01	>0.60	>0.60

each day, minus the amount of energy it must expend to obtain that food divided by the time spent foraging. Since this ratio measures the net energy gain per unit time foraging, natural selection should maximize foraging efficiency if energy is limiting and also if other factors that can affect individual fitness (e.g., predation) do not influence feeding behaviour (Schoener 1971; see below). Two ratios were calculated (Table 5): a "feeding" efficiency ratio, that considers only the time and energy expended while actually feeding, and the "foraging" efficiency ratio that includes the cost of both feeding and moving between food patches. There were significant differences between groups in the mean daily feeding efficiency: individuals in the smallest group obtained significantly more net energy per minute of feeding time than did the members of the two larger groups (Duncan's multiple range test after ANOVA, $P < 0.05$).

This result reflects the fact that although the members of the small group spent only one-half as much time (and energy) per day feeding (Fig. 1 and Table 4), they obtained almost the same total amount of food and energy as did the members of the larger groups (Table 3). However, the individuals in the small group spent more time and energy moving per day, and when both foraging costs are included, the mean foraging efficiency ratios of the three groups were not significantly different from each other. These results emphasize the importance of including the costs of both feeding and movements in studies of foraging efficiency under natural conditions.

Table 5 also includes a mean energy balance ratio for the members of each group. This ratio is defined as total energy intake on one day divided by total calculated energy expenditures on the same day, and it is an estimate of the ability of an animal to obtain sufficient food to meet its energy requirements. Although the mean ratio of the members of the smallest group was slightly lower than that observed in the two larger groups, this difference was not statistically significant. The mean ratios of all of the baboons examined was greater than one, suggesting each was able to achieve positive energy balances during the study. However, the mean ratio of the three adult males, when considered together as a class, was significantly lower than those of either type of female; the observed values were 1.16 ± 0.15 ($\bar{x} \pm \text{SE}$) for adult males, 1.71 ± 0.22 for the three pregnant females, and 1.91 ± 0.16 for the three females with infants ($F=5.51$, $df=2,6$; $P<0.05$; F ratio for the main effect of sex-reproductive class was determined using the focal animal-within-class as the error term). This difference was the result of the fact that the mean daily energy intake of each class of female, when examined on a per kilogram of body mass basis, was significantly higher than that of the males (Duncan's multiple range test, $P<0.05$; overall $F=9.32$; $df=2,6$; $P<0.01$), while there were no significant differences between classes in the estimated daily energy expenditures per kilogram of body mass (absolute expenditures were, of course, greater in the heavier males). Pregnancy and lactation place additional energy demands on females, and the estimates of energy expenditure as calculated above do not include the costs of reproduction by these animals. The fact that both classes of females had significantly higher energy balance ratios than did the males suggests that they are able to achieve higher rates of food and energy intake during foraging in response to these additional energy requirements.

Other behavioural differences between groups

In addition to foraging efficiency, predation pressure has been widely suggested to be an important influence in the evolution of social organization among primates and other animals (e.g., DeVore and Hall 1965; Crook 1972; Eisenberg et al. 1972; Rowell 1979, van Schaik 1984). Individuals could benefit from living in groups if the probability of detecting a predator is greater when more animals are searching for predators (the "many eyes" hypothesis: e.g., SA Altmann 1974; Treisman 1975), by actively deterring predators through cooperative defense or mobbing, or other mechanisms (see Alexander 1974). Large predators are common at Amboseli; those known or suspected to take baboons include lions (*Panthera leo*), leopards (*P. pardus*), spotted hyenas (*Crocuta crocuta*), and possibly large eagles and pythons (*Python sebae*) (Altmann and Altmann 1970; Stelzner and Strier 1981). The baboons typically give alarm vocalizations when a potential predator is detected, and they often rapidly move away from the predator or climb trees if lions are present. Although all of the groups frequently gave alarms, there were no deaths during this study that could be definitely attributed to predation (two members of the large group disappeared during the study; whether or not they were killed by predators is unknown). It was therefore not possible to directly test the hypothesis that members of larger groups are more likely to avoid predation than individuals living in smaller groups. However, since predation can be an important selective force even when it is a relatively rare occurrence, I examined several aspects of the behaviour of individuals living in different-sized groups that might reflect differential susceptibility to predation.

First, if members of small groups are less likely to discover or deter an approaching predator, one solution would be for the individuals in these groups to attempt to remain near large trees so that they could quickly escape any non-climbing predator, such as a hyena or lion, that was able to approach close to the group before it was discovered. I estimated distance from the focal animal to the nearest tree >10 m during point samples taken 30 s before and after each focal sample. Mean distance to such trees was a function of group size: the members of the smallest group tended to stay nearest to large trees during the day ($\bar{x} \pm \text{SE} = 24 \pm 2$ m), while those in the two largest groups were most likely to be found in more exposed locations (29 ± 2 m and 32 ± 2 m respectively; $F=5.24$, $df=2,1013$, $P<0.01$).

A second difference in the behaviour of the groups that may be related to predation involves the use of elevated locations for resting during the day. By sitting above the ground when not foraging or moving, an individual will have a larger field of view around it, and it would be more likely to locate any nearby predators (it would also be less susceptible to any terrestrial predator that did approach). I divided resting time in the focal samples into three different categories based upon the height of the animal above the ground: resting in contact with the ground, resting less than one meter above the ground, or resting at heights one meter or more above ground level (usually within a tree). Individuals in the smallest group (Limp's Group) spent significantly more time resting in elevated locations one meter or more above the ground (55% of daily rest time vs. 19% in Hook's Group and 13% in Alto's; $F=5.85$; $df=2,6$; $P<0.05$), while individuals in the two larger groups spent significantly more time resting on the ground (33% vs. 67% and 78% respectively; $F=10.71$; $P<0.05$). The tendency of animals in the small group to rest in elevated locations was particularly apparent in the behaviour of the adult male Caesar, who would frequently sit in a tree or on top of a dead tree stump apparently scanning for predators (or other baboons) as his group moved through their home range during the day. This "sentry" behaviour was observed much less commonly among the males of other groups; whether or not it is typical among small baboon groups in general is unknown.

I did not determine the distribution of predators or trees within the home ranges of the groups. However, it is likely that these results reflect differences in choice of location between Limp's Group and the other groups, either through using available vegetation within their home range, or by occupying a range that had a high density of cover. Although indirect, these data are consistent with the hypothesis that baboons in a small group may be less able to detect approaching predators than individuals in larger groups, and that they may attempt to compensate for this by resting above the ground and by remaining nearer to large trees in order to escape quickly if a ground predator does approach the group. Definitive tests, however, will require a long term analysis of actual predation patterns in different groups of various sizes.

Discussion

The analyses given above indicate that baboons living in groups containing 33 and 44 members

did not achieve a statistically significant higher average foraging efficiency ratio during this study than did individuals in a group that had only 8 members. The methods used in this study to calculate energy intake and energy expenditures required using a number of approximated or estimated values; however, since the same numbers were used for all animals, this should not drastically affect comparisons made between groups. Since energy may be stored physiologically as lipids and carbohydrates, even small differences in the daily rate of energy accumulation over expenditures could lead to substantial absolute differences over long periods of time, and could have important biological consequences for the individuals living within each group. It may be difficult to disprove the hypothesis that there is an optimal group size for foraging efficiency within any population, since it is often impossible to determine a priori the magnitude of differences in efficiency that are biologically significant. Further, size effects may become important only under certain conditions; for example, periods of food stress or when obtaining particular food types (see below). However, the results of this study suggest that increased foraging efficiency should not be assumed to be an important advantage of group foraging in any species unless greater efficiency actually can be demonstrated through field analysis. Further, it illustrates the importance of attempting to estimate (however crudely) actual energy values, rather than relying on indirect variables such as time spent foraging.

Van Schaik et al. (1983) examined the relationships between group size and foraging behaviour in the long-tailed macaque (*Macaca fascicularis*). These authors compared the time-activity budgets of free-living individuals that were observed in groups ranging in size from between 10 and 34 members. They found that the estimated median percentages of time spent both searching for food and traveling (i.e., "moving" in the present study) increased with group size, while the time spent actually feeding decreased. Although no estimates were made of either energy expenditures or energy intake during feeding, the observed differences in the time budgets are consistent with the hypothesis that food competition is greater in larger groups of macaques, and the authors conclude that feeding advantages do not appear to be the primary factor favoring group living in this species.

The members of the smallest group (Limp's) spent only one-half as much time feeding per day as did individuals in the larger groups (Fig. 1), but

they were able to obtain almost the same amount of food during that time through a relatively higher rate of food intake. They also spent substantially more time resting and moving through their home range. In contrast, individuals in the two larger groups spent more time feeding (but ingested food at a lower rate), and spent less time resting or moving. Whether these differences in time budgets and feeding rates reflect differences in the distribution or abundance of food resources in the non-overlapping portions of the three groups' home ranges is unknown. The three groups utilized a combined area of over 31 km² during this study, and fed upon a total of 40 different plant and animal species. The distribution of many of these species is highly patchy at Amboseli, and I was not able to sample their abundance over the entire area used by the baboons. Yet it is in precisely this type of habitat that any benefits from information-sharing among group members about the location or quality of food patches should be most apparent. Since the groups did not defend territories, they did have access to exactly the same resources in the areas of home-range overlap during at least a portion of their foraging time (see description of home ranges, above). However, if the differences observed in this study reflect only differential characteristics of the resources in each home range, these data suggest that the smallest group actually occupied the range with the richest food patches, since they were able to obtain almost the same amount of energy as the members of the two larger groups, while only feeding for half the length of time.

A second possible explanation for these results is that if individuals in a small group were less likely to detect or avoid predators, they might attempt to minimize the amount of time spent feeding, when they may be most susceptible to predation, and to stay closer to trees during the day. In contrast, baboons in larger groups may be able to spend more time feeding because predators are more likely to be detected before they are able to move close to the group, and they also are able to utilize areas further from escape routes. The members of the larger groups did not actually obtain significantly more energy per day during this study than those in Limp's Group, but the ability to feed for long periods in open areas could become important during periods of nutritional stress. For example, during the dry season, many of the fruits and seeds from bushes and trees that were important parts of all groups' diets during this study are not available. The primary dry season foods of the baboons are corms of various

grass species (S.A. Altmann, personal communication). The corms most commonly eaten are found in open areas (particularly *Sporobolus kentrophyllus*). Corms must be dug out of the ground, and require considerable time to process. Thus, during the dry season, individuals in small groups may be required to choose between foraging in open areas where the risk of predation may be high, or remaining near cover where there may not be enough food. A comparison of feeding locations and energy intake rates in different sized groups during the dry season would be of considerable interest.

The fact that individuals in Limp's Group were able to obtain only slightly less energy per day while feeding for only half as much time as those in the two other groups indicates that feeding-time budgets may be extremely poor predictors of actual rates of food and nutrient intake. Feeding-time data alone (e.g., many papers in Clutton-Brock 1977) should therefore be used with caution even when comparing different groups of the same species living together in the same habitat. In addition, although the baboons in each group spent similar proportions of time feeding on each general food class (Table 2), the actual overlap in the diets of the three groups when analyzed on the basis of individual species was quite low. The reasons for the latter finding are not clear. As mentioned previously, the distributions of many plant species at Amboseli are patchy, and it is likely that the groups did not have equal access to all species in the areas of their home ranges that did not overlap with the other groups. Some of the foods eaten by the baboons were available only on a seasonal basis, and although this sampling was rotated between each group every 4–5 days, this factor also might have affected the observed patterns. For whatever reason, the fact that the diet similarity values recorded during this study ranged between only 0.476 and 0.588 for groups on adjacent and overlapping home ranges means that reliable generalizations about the species composition of the diets of omnivorous primates may be difficult to achieve on the basis of studies of only one group.

The mean estimated daily food intake of all animals observed was 27.53 g dry mass per kilogram of body weight. The mean PFV energy influx was estimated to be 385 kJ kg⁻¹day⁻¹. There have been few other attempts to measure energy intake among free-living primates, and it is not presently possible to compare these values with information obtained by using similar methods for other species. Nagy and Milton (1979), however, directly measured the energetics of food consumption in

three captive howler monkeys (*Alouatta palliata*) in Panama. They found that the howlers consumed food from a natural diet containing an average of $1,020 \text{ kJ kg}^{-1}\text{day}^{-1}$, of which a total of 665 kJ kg^{-1} was not assimilated and was lost in the feces or urine. This yielded a total of $355 \text{ kJ kg}^{-1}\text{day}^{-1}$ that was available for metabolic purposes. This value is only 30 kJ or 7% lower than the estimated PFV energy influx of $385 \text{ kJ kg}^{-1}\text{day}^{-1}$ for the baboons during this study. The similarity in these two values suggests that different species of primates may have similar energy requirements (per kilogram of body weight) and also that it may be possible to use methods like those employed in this study to reliably estimate energy intake in free-living populations.

The mean estimated daily expenditure of energy for all animals sampled was $238 \text{ kJ kg}^{-1}\text{day}^{-1}$. This value is approximately 57% higher than that predicted from the basal metabolic rate alone, and does not include any energy used for thermoregulation, growth, or reproduction among females. Unlike energy intake, energetic expenditures have been examined in several other primates using methods similar to those of this study. Iwamoto (1979), for example, estimated that daily energy costs for a free-living adult male gelada baboon (*Theropithecus gelada*) in Ethiopia was $179 \text{ kJ kg}^{-1}\text{day}^{-1}$ (calculated from his Table 12.20), while in this study the mean value for males was $219 \text{ kJ kg}^{-1}\text{day}^{-1}$. Iwamoto's estimate for one female was $203 \text{ kJ kg}^{-1}\text{day}^{-1}$; for this study the average for females was $248 \text{ kJ kg}^{-1}\text{day}^{-1}$. Coelho et al. (1976 and personal communication) estimated that howler monkeys in Guatemala expended $362 \text{ kJ kg}^{-1}\text{day}^{-1}$. Their estimate using this method was within 3% of the value obtained by Nagy and Milton (1979) using doubly-labeled water with howlers in Panama ($355 \text{ kJ kg}^{-1}\text{day}^{-1}$). Daily energy expenditures in a species will vary with typical activity patterns and average body weight. Whether these values, which are not radically different from each other, reflect differences in activity or are a function of methodology, remains to be determined.

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