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Author(s): Philip Muruthi, Jeanne Altmann, Stuart Altmann
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Resource base, parity, and reproductive condition affect females' feeding time and nutrient intake within and between groups of a baboon population

Philip Muruthi[1,2], Jeanne Altmann[1,3,4], and Stuart Altmann[1,3]

[1] Institute of Primate Research National Museums of Kenya, P.O. Box 24481, Karen, Kenya
[2] Zoology Department University of Nairobi, P.O. Box 30197, Nairobi, Kenya
[3] Department of Ecology and Evolution University of Chicago, Chicago, IL. 60637, USA
[4] Department of Conservation Biology Chicago Zoological Society, Brookfield, IL. 60513, USA

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Summary. We examined within- and between-group differences in aspects of feeding and nutrient intake among adult females of a single population of baboons *(Papio cynocephalus)* in Amboseli National Park, Kenya. Differences in time spent feeding, daily energy and protein intake and feeding efficiency (nutrient intake per minute spent feeding) reflected differences in resource base, reproductive condition and parity. Baboons that partially fed from a lodge garbage dump spent less than half the time feeding than those that were feeding totally in the wild. During this greatly reduced feeding time, the garbage-feeding group had a similar daily energy intake and only a slightly lower daily protein intake relative to wild-feeding baboons. Consequently, the feeding efficiency of the semi-provisioned baboons was appreciably higher than that of the non-provisioned baboons. For the totally wild-feeding baboons, samples were large enough to permit analyses of feeding time and nutrient intake during different reproductive states and parity. Females spent more time feeding and had higher daily energy and protein intake when they were pregnant or lactating than when they were sexually cycling. Nulliparous females spent more time feeding than their multiparous counterparts. The daily energy intake of nulliparous females was higher than that of their multiparous counterparts, but their daily protein intakes did not differ significantly. Pregnant or lactating and nulliparous females had higher feeding efficiency than their sexually cycling and multiparous counterparts. The two nulliparous females in the garbage-feeding group spent more time feeding but did not take in more energy or protein per day than their multiparous counterparts.

Key words: Baboons – Nutrition – Reproduction – Feeding efficiency

Intraspecific variability in primate feeding behaviour has been related to differences in group size (Stacey 1986), social dominance rank (Wrangham and Waterman 1981; Post et al. 1980), desirability of food (Belzung and Anderson 1986), reproductive condition (Post et al. 1980), age (Post et al. 1980; Clutton-Brock 1977), and sex (Post 1978; Post et al. 1980; Clutton-Brock and Harvey 1977). Deag (1977) suggested that differences in access to preferred food sites, frequency of feeding bout interruption, and time spent in search of food are all possible mechanisms enhancing nutritional intake. Additionally, evidence from several primate studies suggests that direct and indirect competition for food resources within primate species is reduced through ecological segregation among group members that is based on dominance status and on morphological differences that are correlated with age and sex (Clutton-Brock 1977).

Intraspecific variability in feeding behaviour may also result from differences in nutritional requirements that arise from differences in body mass, physiological condition, reproductive status, and amount of time and energy spent in performance of activities. On the basis of the increased metabolic demands entailed by greater body mass (Garland 1983), males usually require more food for self-maintainance; for example, adult male baboons are twice as heavy as females (Altmann 1980). Within-sex differences result when the metabolic requirements of females are elevated by the demands of pregnancy, lactation, and the transport of an infant (Altmann 1980; Altmann and Samuels in press) and when animals are engaged in higher levels of activity (Coelho 1974), such as those resulting from increased travel (Taylor et al. 1982).

The presence of both wild-feeding and semi-provisioned groups of baboons in Amboseli, Kenya, provided an opportunity to examine differences in feeding behaviour and nutritional intake that can arise as result of management practises. We obtained quantitative estimates of feeding behaviour and actual food intakes by semi-provisioned and non-provisioned adult female ba-

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Offprint requests to: J. Altmann

boons, *Papio cynocephalus,* through direct observation of feeding behaviour and through nutritional analyses of food items. We were then able to make comparisons between different groups within the same population that had dissimilar feeding conditions. Differences within each group were also investigated with respect to parity and reproductive condition. In each case, we examined differences in time spent feeding, in resultant intake of two important nutrients, energy and protein, and in efficiency of feeding as measured by protein and energy intake per unit of feeding time. Social aspects of feeding and nutritional intake are addressed elsewhere (Muruthi and Altmann, manuscript).

Methods

Our study subjects were the adult female members of two baboon groups in the semi-arid savannah of Amboseli, Kenya (see Altmann and Altmann 1970; Western and van Praet 1973 for area description). At the time of the study, 18 adult (post-menarche) females were in Hook's Group and 11 in Lodge Group. The wild-feeding group, Hook's Group, had been studied since 1980 (Pereira 1984; Altmann et al. 1985; Altmann and Muruthi 1988) and the semi-provisioned one, Lodge Group, whose members obtained food from a garbage pit, since 1984 (Altmann and Muruthi 1988).

All study group members were habituated to the presence of non-interactive observers. The baboons were identified individually by natural marks and physiognomy. Observations were carried out by following the baboons on foot.

Reproductive condition of females was monitored by recording the size and turgidity of the sexual skin, the color of the paracallosal skin, and the presence of menstrual blood for all adult females on each day that the group was contacted (as in e.g. Altmann and Altmann 1970; Silk 1986).

Food-specific time budgets for each female were obtained from instantaneous (point) samples (Altmann 1974). During 10-min observation periods divided across the daily observation time (0800–1800 hours), each female's activities, as defined in Post (1981), were recorded at one-minute intervals (see Altmann and Muruthi 1988; Muruthi 1989 for further details). In addition, whenever the activity was feeding, the food eaten was recorded. We thereby obtained estimates of the total amount of time that female baboons spent feeding and the amount of time spent eating each food, that is, female-specific and food-specific time budgets. Feeding was recorded whenever the baboon was in direct contact with the food plant.

Daily intakes of energy, of protein, or other nutrients were estimated using a factorial approach (S. Altmann, manuscript), here worded in terms of grams, but suitable, with appropriate change of units, to energy or other components that are expressed in units other than mass. For any nutrient N, the average amount ingested per day by a specified individual was estimated as follows:

$$\frac{\text{grams of } N}{\text{day}} = \sum_i \underbrace{\frac{\text{potential intake minutes on food } i}{\text{day}}}_{A_i} \; \underbrace{\frac{\text{units of food } i}{\text{potential intake minutes on food } i}}_{B_i} \; \underbrace{\frac{\text{grams of } i}{\text{unit of } i}}_{C_i} \; \underbrace{\frac{\text{grams of } N}{\text{gram of } i}}_{D_i},$$

For wild foods, A_i is the individual's time-budget value (minutes per day) for food i, B_i is the unit intake rate of food i, C_i is the unit mass of food i (assumed to be the same for all individuals), and D_i is the concentration of nutrient N in the i th food (also assumed to be the same). We here assume that the covariances between these factors are negligible (Welsh et al. 1988). Estimates for each factor were pooled for each female over the whole study or other period (e.g. when cycling), as appropriate.

Human foods were obtained almost entirely from the lodge's garbage pit and the immediately surrounding area, demarcated by an electric fence. For such foods, "potential intake minutes on food i" in factors A and B represents the number of minutes in the pit area, obtained by recording the time at which the subject entered and left the area.

Unit intake rates (B_i) for wild foods were obtained primarily from past studies on Amboseli baboons (e.g. Post 1978; S. Altmann manuscript; Altmann et al. 1987). When such data were not available for a food, the units of food consumed per minute spent feeding were obtained from separate field samples on adult females. For wild foods, "potential intake minutes on food i" represents the number of minutes of hands-on feeding time on that food. In using these various rates, we assumed both that mean harvesting rates for these foods had not changed and that they were the same for all adult females.

For human foods that the baboons consumed in discrete units, unit intake rates (B_i) were estimated from data gathered by the first author during the study in essentially the same manner as had been done for wild foods: the numbers of bites or individual pieces of the food that the subjects ingested were counted in timed (10-min) samples taken on females during periods when they were in the pit area. If a female left the pit area during such a sample, the sample terminated the moment she left the pit unless she carried food with her, in which case the sample terminated as soon as the food disappeared into her mouth or was discarded.

Unit mass values (C_i) for most wild baboon foods in Amboseli were obtained from S. Altmann (manuscript) and Altmann et al. (1987). For wild foods not included therein and for human foods consumed in discrete plant units, such as mango seeds, samples were obtained in the field and the pooled mean mass of each food item was obtained by counting and weighing representative samples. The nutrient content (D_i) of wild baboon foods were obtained from Altmann et al. (1987); those of human foods from Wohl and Goodhart (1960) and Kirschmann (1979).

For human foods for which the number of bites was the unit of consumption, mean bite mass (C_i) was estimated in the following way, here described in terms of pineapple fruit. In special samples, pre-weighed pieces of pineapple were given to a female and the number of bites were counted. Then, when the female freely left the pineapple, the remnant was retrieved and weighed. Total removed mass in all samples divided by the total number of bites estimates mean bite mass.

For some human foods, the mass in grams of the item ingested could be estimated visually and, whenever possible, the masses of the food items eaten by the subjects were estimated directly at the pit in this way during timed samples. Such estimates of individual-specific food mass intake per unit time provided an alternative to the products of factors B and C in Eq. 1, and when available, were used instead.

To calibrate these visual estimates of mass, the mass of an object was first estimated visually by the observer and then weighed using a triple-beam balance (OHAUS Model 700) to ascertain the accuracy of such estimates. The mean of 26 mass-estimate trials randomly selected from a larger list of estimated and actual masses of items were compared and found not to differ significantly (t-test, $t = 0.318$, $df = 50$, $P > 0.05$).

Hook's and Lodge Group baboons were sample on 96 and 120 days respectively during the 12-month study period between August 1986 and July 1987. The total number of minutes of instantaneous samples (Altmann 1974) for all females studied in Hook's Group was 15,769. Of these, 7,111 were obtained when females were either pregnant or lactating and 8,648 when they were sexually cycling. For Lodge Group females, the total number of point samples was 15,295, of which 11,638 were obtained when females were pregnant or lactating and 3,657 when they were sexually cycling.

Data were entered on a microcomputer at the field site. Food-specific time budgets were computed by use of STATPAK (Northwestern Analytical 1982). SUPERCALC (Computer Associates International 1987) was used to calculate the mean daily energy and protein intakes. Values for statistical tests were computed on a hand calculator. The fiducial level was set at $P = 0.05$, two-tailed, in all tests.

Results

Females of the wild-foraging Hook's Group spent 45.4% and those of Lodge Group 22.6% of their time feeding (Fig. 1), a two-fold difference that was statistically significant (Mann-Whitney *U*-Test, $U_s = 158$, $df = 9{,}18$, $P = 0.001$). However, this very large difference in feeding time was not reflected in the concommitant daily energetic intakes of females in the two groups (*t*-test, $t = 1.864$, $df = 27$, $P > 0.05$). On average, females of Hook's Group and Lodge Group took in 3828.12 and 3456.12 kJ per day respectively (Fig. 1). In contrast, daily protein intake did partially reflect the difference in time spent feeding; mean daily intake for females of Hook's Group was 31.26 g/day and for those of Lodge Group was 20.65 g/day (*t*-test, $t = 6.814$, $df = 27$, $P < 0.05$; Fig. 1).

Finally, we considered efficiency of nutrient intake, i.e. nutrient intake per minute spent feeding. Lines of equal intake efficiency are drawn, one each through the energy and the protein values for Lodge Group (Fig. 1). Because both the energy and protein values for Hook's Group fall below the respective lines through the Lodge Group points, we can see that nutrient intake during Hook's Group's protracted feeding time is much less than would be the case if intake were as efficient in Hook's Group as in Lodge Group. Clearly, females of Hook's Group took in fewer nutrients per feeding minute than those of Lodge Group. The energy intakes were 14.04 and 26.17 kJ/min and the protein intakes were 0.12 and 0.16 g/min for Hook's and Lodge Group females respectively (Fig. 1).

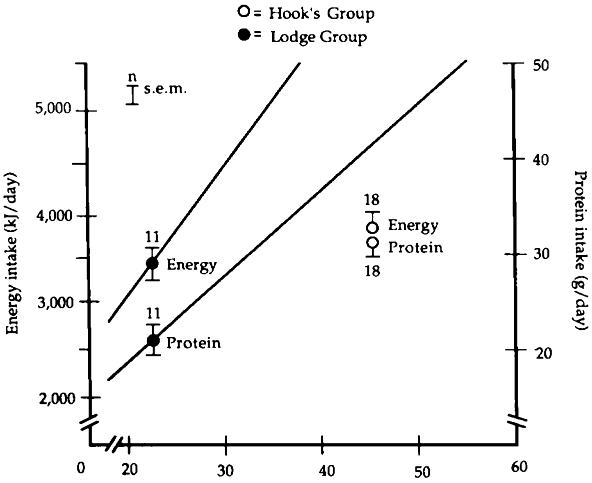

Fig. 1. Daily energy and protein intake by female baboons of Lodge and Hook's Group in relation to the proportion of time spent feeding by each group (mean of values for individuals)

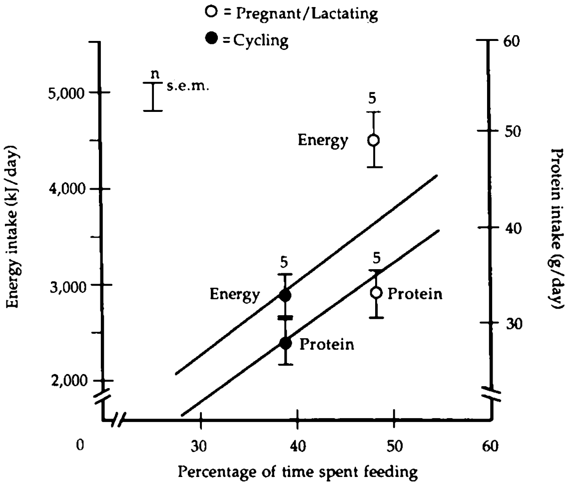

Fig. 2. Daily energy and protein intake by females of Hook's Group as a function of the proportion of time spent feeding for females in different reproductive states

A two-way analysis of variance revealed that considering all females of both groups, feeding time was significantly related to both reproductive condition and parity; females spent more time feeding when they were young (nulliparous), and within each parity, when they were either pregnant or lactating ($P < 0.05$).

Below, we further examine within-group differences in each of the feeding parameters with respect to differences in reproductive condition and parity. The complete analyses could only be done for Hook's Group, although suggestive patterns within Lodge Group are noted where appropriate. Comparable analyses were not always possible for Lodge Group females because sample sizes of intake rates were not adequate in all reproductive states and parities; females of Lodge Group experienced shorter adolescent sub-fertility and consequently spent less time as cycling nullipara; in addition, they usually conceived again during the first cycle after termination of postpartum amenorrhoea (Altmann et al. manuscript).

Within Hook's Group feeding was related to the reproductive state of the female. Overall, females of Hook's Group spent more time feeding when they were pregnant or lactating than they did when they were sexually cycling (*t*-test, $t = -2.53$, $df = 23$, $P < 0.05$; Fig. 2). The daily energy intake of Hook's Group females when they were lactating or pregnant was 4534.28 kJ/day, 57% higher than when the same females were cycling (*t*-test, $t = 4.481$, $df = 8$, $P < 0.001$; Fig. 2). In contrast, the daily protein intake by females when they were cycling was not significantly different from that when they were pregnant or lactating, 27.9 and 33.2 g protein, respectively (*t*-test, $t = -1.421$, $df = 8$, $P > 0.05$; Fig. 2). Pregnant or lactating females of Hook's Group not only took in more energy and more protein than they did when cycling, but they were more efficient in doing so in the case of energy, with rates of 15.77 kJ/min and 12.89 kJ/min, respectively (Fig. 2). Females took in 0.12 g protein per min both when they were pregnant or lactating and when they were sexually cycling (Fig. 2).

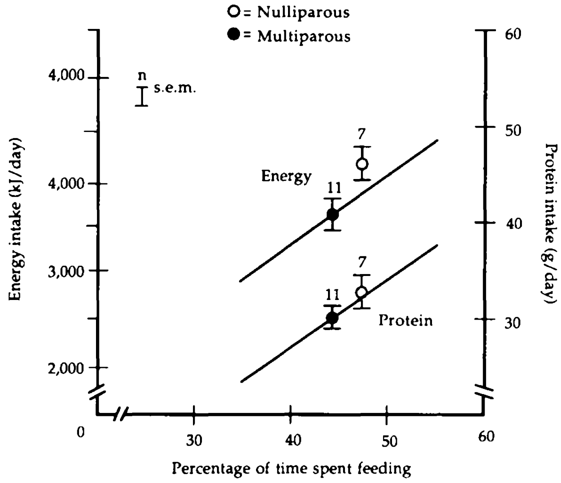

Fig. 3. Daily energy and protein intake by nulliparous and multiparous females of Hook's Group as a function of the proportion of time spent feeding by females of each parity class

Females of Lodge Group also spent more time feeding when they were pregnant or lactating than when they were sexually cycling. However, no comparisons could be made on both daily energy and protein intakes due to inadequate samples of food intake in different reproductive states.

Nulliparous females in Hook's Group spent significantly more time feeding than their multiparous counterparts (t-test, $t=4.632$, $df=16$, $P<0.01$; Fig. 3). They took in 17% more energy than multiparous females of the same group (t-test, $t=2.777$, $df=16$,0 $.01<P<0.05$; Fig. 3). Nulliparous and multiparous females did not differ significantly in daily protein intake (t-test, $t=2.120$, $df=16$, $P>0.05$; Fig. 3), i.e. the significant difference in proportions of time spent feeding was not reflected in daily protein intake. Nulliparous females of Hook's Group had somewhat greater efficiency of energy intake; they took in 14.88 kJ/min in contrast to 13.50 kJ/min for multiparous females (Fig. 3). The protein intake was 0.12 g/min for nulliparous females and 0.11 g/min for multiparous ones (Fig. 3).

The two nulliparous females of Lodge Group spent more time feeding, but their daily energy and protein intakes were lower than those of multiparous females, and their feeding efficiences were 13.03 kJ and 0.08 g/min of feeding for energy and protein intake respectively.

Discussion

Time devoted to feeding by adult females in the two study groups reflected differences in the food resources available in their respective home ranges. The semi-provisioned baboons of Lodge Group spent significantly lower proportions of time feeding than did the non-provisioned, wild-feeding ones of Hook's Group. The foods of the Lodge Group females were acquired and processed more easily, and probably had higher digestibility because of lower crude fiber content (see Iwamoto 1988), than the wild foods, which were patchily distributed (Post 1982) and hard to process (see Rhine and Westlund 1978; Rose 1976). Similar differences have been reported for feeding time in comparisons between provisioned and non-provisioned vervet monkeys, *Cercopithecus aethiops*, also in Amboseli (Brennan et al. 1985; Lee et al. 1986), olive baboons, *Papio anubis*, at Gilgil, Kenya, (Musau and Strum 1984; Quick 1984, 1986), rhesus monkeys, *Macaca mulatta*, in India (Malik 1986; Seth and Seth 1986). When females of Hook's and Lodge Group were studied solely during the end of two dry seasons, one of which followed a drought year, the differences in feeding time between feeding conditions was even greater than that found during the continuous 12-month all-season study reported here (c.f. Altmann and Muruthi 1988) as would be predicted.

In the present study, differences in feeding time between groups did not translate simply into concomitant differences in nutrient intake. Although the females of Lodge Group spent less than half as much time feeding as did those of Hook's Group, they were more efficient and obtained the same amount of energy and only slightly less protein in the much-reduced feeding time. They did this by taking advantage of the garbage pit foods that were spatially concentrated, easy to extract and process, more calorically concentrated and more readily digested in comparison to the wild foods. Comparable data for nutrient intake are not available from these other studies [but see Stacey (1986) for a comparison among three wild-feeding baboon groups primarily during a wet period in Amboseli]. Time itself may often be an important variable, and the time spent on foraging affects energetic expenditure and restricts time available for other activities. Nonetheless, when nutrient intake is the focus of comparisons, overall feeding time alone will often be misleading as an indicator of differences in comparisons among species, populations, or even individuals that differ considerably in conditions or characteristics of nutrient intake (Stacey 1986).

In the present investigations, significant differences in feeding time within groups emerged when variability in reproductive condition was considered. Pregnant and lactating females in each group spent more time feeding than did cycling ones; this appears to be the rule rather than an exception among primates and has been reported for other mammals, e.g. red deer *Cervus elaphus* (Clutton-Brock et al. 1982), pandas *Auluropoda melanoleuca* (Schaller et al. 1985). The increased feeding time of pregnant and lactating females in the present study resulted in greater daily energy yields per day. The total intake difference was greater than expected from the increased time spent feeding. When females in the non-provisioned group were pregnant or lactating, they were more energy efficient in their feeding; that is, through differential selectivity of higher energy foods, they obtained higher energy yields, than when cycling. Although there was also a trend toward higher protein intake, this did not reach statistical significance. Higher energy intake was achieved both by increasing feeding time and by selecting higher energy foods, perhaps at the cost of high protein foods. Because we were not also able to monitor individual differences in bite rates within the non-provisioned group, we could not evaluate whether bite-rate differences might also affect feeding efficiency.

Parity provided an additional source of feeding variability within groups. In both groups, nulliparous females spent consistently more time feeding than did multiparous ones. For the nulliparous females of Hook's Group this additional feeding time resulted in higher energetic intake. Because nulliparous females were not of full adult size, they were not only obtaining more energy per day but also more energy per unit of body mass; this additional caloric intake would then have been available for completing the growth process and accumulating sufficient fat deposits for reproduction. In Lodge Group by contrast, greater time spent feeding by nulliparous females did not result in higher caloric intake; there, the two young females had to work longer to obtain the same intake as multiparous females. Feeding competition is greater among the semi-provisioned animals (Muruthi 1989; Muruthi and J. Altmann manuscript). Our work in progress suggests that in the semi-provisioned group the disparity in body mass between nulliparous and multiparous females is greater, and adult dominance rank is attained at a later stage relative to reproductive maturation, than for unprovisioned animals. These several factors probably restrict the extent to which young females in the semi-provisioned group could profitably increase food intake.

The present study revealed complex relationships between and within groups among characteristics of feeding behaviour and nutrient intake within a population. Although measurement of various parameters of feeding provided insight into these relationships and allowed better estimation of nutrient intake (Hladik 1977; Whitten 1982) than is usually available, estimations and pooling were still necessary. In particular, we were only able to measure individual differences in feeding rates for the pit foods; for wild foods, available time dictated not only the use of values that were pooled across individuals, but also use of some values from prior research. The conditions under which differences in feeding rates exist and the stability and magnitude of such differences remain unknown, but a short-term study by Stacey (1986) demonstrated between-group differences in intake rates, suggesting the potential profitability of further investigation in this direction. Finally, the possibility that individual animals, or the same animal at different ages, may also exhibit differences in item selectivity within particular food plant species, was beyond the scope of the present study. Selectivity based on nutrient requirements or deficiencies is known for humans and demonstrated experimentally for other animals (Rozin 1976); selective and flexible omnivores such as baboons would be likely candidates for similar behaviour.

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