

Activities and Feeding Behavior of Free-Ranging Pregnant Baboons

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*The activities and feeding behavior of pregnant baboons, *Papio cynocephalus*, were studied in two free-ranging groups in Amboseli National Park, Kenya. Both the environmental conditions and the age of their fetuses influenced females' activity budgets and feeding behavior. Females fed more and rested less during the dry season than during the wet season, and most females spent progressively more time feeding and less time grooming than expected (based upon the amount of recent rainfall) as their fetuses matured. During the wet season, females also devoted significantly greater proportions of feeding time to consumption of grass blades, leaves, and flowers and significantly smaller proportions of their feeding time to feeding upon seeds, corms, and fruit. As their fetuses became older, the proportion of time spent feeding upon seeds increased, and the proportion of time spent feeding upon grass blades and fruit declined.*

KEY WORDS: baboon; pregnancy; feeding; nutrition.

INTRODUCTION

Studies of primate females have focused upon their sexual behavior, mate choice, and interactions with their infants. However, during a substantial fraction of their adult lives females are neither sexually cycling nor lactating; they are pregnant. Baboon females, who give birth at approximately 2-year intervals (S. A. Altmann and J. Altmann, 1970; Ransom and Rowell,

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1972; J. Altmann, 1980; Nicolson, 1982; Strum and Western, 1982), are pregnant for nearly one-quarter of their adult lives. Yet we know very little about the behavior of pregnant females. This report describes changes in the activities and feeding behavior of free-ranging pregnant female baboons, *Papio cynocephalus*, in Amboseli National Park, Kenya.

The energetic needs of mammalian females are profoundly altered during pregnancy by the demands of their maturing fetuses. Female baboons give birth to infants that weigh approximately 7% of their own weight (Leutenegger, 1973; Snow, 1977; J. Altmann, 1983). In addition, mothers must meet the metabolic costs associated with maintaining the products of conception; with carrying the extra weight of the fetus, placenta, uterine tissue, and fluids; and with building fat stores in anticipation of lactation. Nonhuman primate females require approximately 25% more protein than females that are not pregnant and not lactating (Portman, 1970). The metabolic demands of pregnancy intensify as the fetus matures. Primate fetuses gain weight most rapidly during the final third of pregnancy (Tanner, 1970; Hytten, 1980), and it is then that maternal metabolic requirements increase at the highest rate.

Experimental studies of rhesus macaques (*Macaca mulatta*) have demonstrated the effects of nutritional deprivation during pregnancy. When rhesus females are maintained on low-protein diets, they gain less weight and weigh less at the time of delivery than females maintained on diets that contain more protein and equal numbers of calories (Kohrs *et al.*, 1976; Riopelle and Shell, 1978). When pregnancy is terminated at a uniform gestational age, an association can be established between the composition of the mother's diet during pregnancy and the weight of her infant at birth. Mothers maintained on high-protein diets generally produce larger infants (Cheek *et al.*, 1976, Kohrs *et al.*, 1976; Portman *et al.*, 1977). Females maintained on low-protein diets during pregnancy, and allowed to carry their pregnancies to term, gave birth after longer pregnancies than females maintained on high-protein diets, although the birth weights of infants produced by females in these two groups did not differ substantially (Riopelle, 1982; Riopelle and Shell, 1978).

As the metabolic requirements of pregnancy increase, the behavior and/or diet of females is likely to change. To increase their intake of energy, protein, or other important nutrients, females may increase the proportion of time they spend feeding. However, females might also achieve similar metabolic profits by reducing their levels of activity and maintaining stable levels of food intake (J. Altmann, 1980; Hytten, 1980). Limited data on the feeding behavior of baboons in Amboseli during one dry-season period suggest that pregnant females spent more time feeding than nonlactating adult females (Post *et al.*, 1980). Pregnant baboons at other sites also tend to in-

itiate fewer social interactions (Saayman, 1972) and maintain a greater distance from other group members than do nonpregnant females (Collins, 1984). Collins (1984) suggests that pregnant females, by remaining on the periphery of their group, minimize interference during feeding and may thereby enhance their rate of food intake. It is also possible that, if females are able to discriminate among food items of different nutritional value, they may alter the composition of their diet as their metabolic demands change.

The activity budgets and diet of pregnant females in Amboseli might also have been affected by seasonal changes that occurred during their pregnancies. In Amboseli, rainfall is typically concentrated during two periods: the "short rains" usually fall between November and December, and the "long rains" usually fall between March and May. A prolonged dry period typically begins in June and lasts through October (S. A. Altmann and J. Altmann, 1970). During the present study period, the short rains were particularly heavy, and little rain fell during the normal months of the long rains. Conceptions were clustered during the wettest part of the study, and it became drier as most females' pregnancies progressed (Silk, 1986). The baboons' diet is more diverse and their foods are more abundant during the wet season than during the dry season (Post *et al.*, 1980). Surface water, which baboons drink daily, becomes plentiful. Lactating female baboons in Amboseli spent less time feeding following wet months than following dry months (J. Altmann, 1980). The activity budgets and diets of females might have changed systematically in response to these changes in environmental conditions.

There are also several factors that may have contributed to variation in the activities and feeding behavior among pregnant females. The subjects of this study were drawn from two social groups, Alto's Group and Hook's Group. These groups traveled in different areas, although there was some overlap in their home ranges. The two groups also differed in their size and demographic composition. The focal females constituted a heterogeneous sample with respect to their age, parity, and dominance rank. Some previous studies have shown that high-ranking primates obtain priority of access to desirable food resources and that the diets of high- and low-ranking females sometimes differ (Wrangham, 1981; Whitten, 1983; Whitten and Smith, 1984). Although Post *et al.* (1980) found little evidence that dominance rank influenced the feeding behavior among the females of Alto's Group during one dry season, a larger set of data collected over a longer time period might produce different results. Maternal parity and age might also influence activity budgets. Female monkeys conceive for the first time approximately 1 year after they have reached menarche and may not have attained their full adult weight at the time of their first conception (J. Altmann *et al.*, 1987; Lancaster, 1984). The nutritional needs of young, primiparous females may therefore exceed those of older, multiparous females.

Finally, females may have been affected by the sex or viability of their fetuses. In captivity, cercopithecine male infants generally have higher birth weights than newborn females (DiGiacomo *et al.*, 1978; Riopelle and Shell, 1978; Coelho *et al.*, 1984; Sackett *et al.*, 1975). If this sex difference is also characteristic of free-ranging baboons, females carrying male fetuses may have higher metabolic requirements than females carrying female fetuses and may adjust their activity budgets accordingly. Three infants who were born after pregnancies that lasted 154, 184, and 209 days did not survive the first week of life. It is possible that the behavior of females carrying nonviable fetuses may have differed systematically from that of females carrying healthy fetuses.

The analysis that follows focuses upon changes in the behavior of individual females over the course of their pregnancies, and attempts to identify sources of variation in activities and feeding behavior among females. The primary objective of the present study was to document how the activities and feeding behavior of females changes between conception and parturition, not to compare explicitly the behavior of pregnant and nonpregnant females. Therefore, no information about the behavior of lactating or cycling females was collected.

SUBJECTS AND METHODS

Study Population and Sites

Two groups of free-ranging and unprovisioned yellow baboons, *Papio cynocephalus*, were studied in Amboseli National Park, Kenya, from December 1982 through September 1983. At the beginning of the present study, Alto's Group was composed of 52 baboons (8 adult males, 4 subadult males, 19 adult females, 10 immature males, 11 immature females), and Hook's Group contained 39 individuals (7 adult males, 1 subadult male, 14 adult females, 8 immature males, and 9 immature females). By the end of the study period, Alto's Group had increased to 63 individuals, and Hook's Group had increased to 44 individuals.

Subjects

All females that were pregnant when the study began, or became pregnant during the study period, became subjects of focal animal observations (J. Altmann, 1974). These females included 15 of the 19 adult females (79%) in Alto's Group and 10 of the 14 adult females (71%) in Hook's Group (Table I).

Table 1. Subjects of Focal Observations

Female	Date of conception of infant	Date of birth of infant	Average rank	Parity	Sex of infant	Status of infant ^a	Days observed
Alto's Group							
Safi	1-9-82	20-2-83	0.94	1	F	LB	7
Fanny	18-10-82	22-3-83	0.33	2	M	NN	10
Eno	1-11-82	22-4-83	0.06	1	M	LB	15
Slinky	27-11-82	26-5-83	0.29	7	M	LB	19
Cete	10-1-83	5-7-83	0.68	3	F	LB	19
Dotty	10-1-83	5-7-83	0.83	2	F	LB	19
Spot	18-1-83	21-7-83	1.00	5	F	NN	26
Oreo	23-1-83	25-7-83	0.28	0	F	LB	25
Vec	24-2-83	21-9-83	0.55	4	F	SB	28
Handle	5-3-83	3-9-83	0.21	5	F	LB	20
Preg	21-3-83	9-9-83	0.32	7 ^b	M	LB	17
Janet	30-3-83	18-9-83	0.00	2	M	LB	17
Vixen	31-3-83	25-9-83	0.32	0	M	LB	19
Summer	7-5-83	26-10-83	0.78	1	F	LB	15
Nazu	13-6-83	11-12-83	0.63	2	F	LB	10
Fanny	23-6-83	17-12-83	0.15	3	F	LB	10
Hook's Group							
Nubbin	10-10-82	24-3-83	0.00	4 ^b	F	LB	14
Lamu	9-12-82	1-5-83	0.36	0	F	LB	19
Pindua	22-1-83	19-7-83	1.00	5 ^b	M	LB	21
Neena	25-1-83	17-7-83	0.68	1	F	LB	18
Lista	13-2-83	1-4-83	0.85	5 ^b	?	AB	4
Moja	15-3-83	4-9-83	0.17	2	M	LB	16
Kupima	17-3-83	11-5-83	0.50	0	?	AB	4
Lista	26-4-83	23-10-83	0.83	6 ^b	F	LB	15
Penny	30-4-83	20-10-83	0.25	1	F	LB	14
Willy	23-5-83	14-11-83	0.92	1	F	LB	11
Kupita	17-7-83	10-1-84	0.58	4 ^b	F	LB	6

^aLB, survived more than 6 months; NN, died within 1 week of birth; SB, died at birth; AB, fetus aborted before term.

^bParity may be underestimated for females that were multiparous adults when the groups were habitated.

Behavioral Data Collection

This study is based mainly upon focal-animal observations of pregnant females. Three focal females were observed on each day that focal data were collected. Each female was observed for four 20-min periods distributed at approximately 2-hr intervals throughout the day. The first observation of the day began at 0740, often before the baboons had descended from their sleeping trees, and the last observation of the day ended at 1700, before the baboons entered their sleeping trees. These four 20-min samples collectively constitute a single "female day" in the analysis reported below. When a female became pregnant, she was immediately inserted into the list of subjects, and when a female gave birth she was dropped from the list. An effort was made to ensure that individual females did not consistently occupy the same position in the daily observation order. The length of the interval between female days varied as the number of pregnant females changed (average interval, 7.6 days). The number of days upon which each female was observed is listed in the last column in Table I.

During focal observations, the activities of the focal female were recorded on a continuous basis. The behaviors that figure in this report are feeding, resting, moving, and grooming. Feeding was recorded when the animal manually or orally manipulated a food item. Chewing on food items that were wholly contained in the mouth was not scored as feeding because it was often difficult (a) to determine when animals had swallowed a food item and (b) to identify food items that had been carried in the mouth for some time before they were eaten (cf. Shopland, in preparation; Altmann, in preparation). Resting is defined as sitting or standing without movement or sleeping. Moving includes all forms of walking, running, and climbing. Grooming includes both self-grooming and allogrooming. For the purposes of this report, all other activities and social interactions are combined within the category of "other." When it was impossible to determine what the focal female was doing, an entry was made to this effect. Out-of-sight time during completed samples accounts for only 0.5% of all focal observation time (total, 547.6 hr). [For more detailed information about observation techniques, see Silk (1986).]

The proportion of time devoted to each of these activities was determined for each female on each day of observation by calculating the number of seconds that elapsed between the time one activity started and the time the next activity began. Since more than one activity rarely occurred simultaneously, each of the behaviors described here (feeding, grooming, resting, moving, other, and unknown) was treated as a discrete activity state in the analyses that follow. Since females' activities were unknown for only 0.5% of all observation time, the inclusion of periods when activities were unknown in the estimate of total observation time has little effect upon the results.

Supplementary Information

All demographic changes (births, deaths, disappearances, immigrations, injuries, and illnesses) and the reproductive condition of adult females were recorded each time the group was contacted by any of the three investigators (A. Samuels, R. S. Mututua, and the author) who were then participating in the longitudinal study. Agonistic interactions were recorded *ad libitum* in a standardized format by all investigators throughout the period of contact with the group.

Observations of dyadic agonistic interactions with clearly decided outcomes were used to establish the dominance hierarchy among adult females (cf. Hausfater, 1975; Walters, 1980). Normally, individuals are assigned ordinal dominance ranks that "correspond" to the number of individuals that dominate them. Such measures are problematic when individuals from groups of different sizes are compared. Hence, dominance rank is expressed here as the fraction of individuals dominated (see Silk, 1986).

A number of females in Alto's Group experienced changes in their relative dominance rank during the study period (Samuels *et al.*, 1987). Each female's weighted average rank during pregnancy was computed by summing the proportion of females dominated during each month in which she was observed during pregnancy and dividing by the number of months observed. This measure is termed "average rank" hereafter.

Statistical Analysis

The statistical analyses described below involve both continuous variables, such as gestational age and the proportion of time spent in a given activity, and categorical variables, such as group membership and fetal sex. To analyze the relationship between two continuous variables, Pearson's correlation coefficients or one-dimensional linear regressions were computed. To analyze the association between one categorical variable and one continuous variable, *t* tests were performed. All statistical analyses were performed by SPSS/PC.

Infant mortality complicated the present analysis because it was possible that the viability of the fetus affected the behavior of the mother during gestation. Therefore, two samples were created for each of the analyses reported below. One sample included all pregnancies, while the second sample was limited to pregnancies that resulted in surviving infants. In general, the viability of the fetus appeared to have little effect upon the activities or feeding behavior of pregnant females. Therefore, only the results from the sample of all pregnancies are presented below, except for the few cases when the results from the two samples differed.

RESULTS

Activity Budgets During Pregnancy

Pregnant females in both groups spent substantially more time feeding during daylight hours (40%) than they spent moving (27%), resting (21%), or grooming (9%) (Fig. 1). Females participated in a number of social interactions other than grooming (e.g., huddling, aggression, play, and interacting with infants), but grooming occupied a larger proportion of observation time than did all other social interactions combined (3%). Together, feeding, moving, resting, and grooming accounted for 97% of all observation time (total, 547.6 hr).

Changes in Activity Budgets During Pregnancy

Females spent significantly more time feeding ($r = 0.1322$, $P = 0.003$, $N = 418$ female days in all analyses) and less time grooming ($r = -0.0914$, $P = 0.031$) as their pregnancies progressed. However, there were no consistent changes in the proportion of time spent resting ($r = 0.0285$, $P = 0.280$) or moving during pregnancy ($r = -0.0012$, $P = 0.491$).

The amount of recent rainfall, defined as the amount of rain that had fallen during the previous 30 days, was also related to females' activity budgets. Females spent significantly less time feeding ($r = -0.2787$, $P < 0.001$) and more time resting ($r = 0.2916$, $P < 0.001$) as the amount of recent rainfall increased. Recent rainfall had no statistically significant effect upon the daily proportion of time spent moving ($r = -0.0416$, $P = 0.198$) or grooming ($r = -0.1422$, $P = 0.211$).

In these analyses, each female day is treated as an independent data point. While the average interval between observations of a single female was more than 1 week, female days may not be statistically independent. If female days are not independent, the size of the sample would be inflated, and the significance of the correlation coefficients may be exaggerated. In order to determine whether the results cited above accurately reflect changes in the behavior of individual females, the relationship between recent rainfall and the proportion of time devoted to each of these activities was calculated separately for each female that was observed during the latter two-thirds of pregnancy.

Thirteen of these 15 pregnant females spent less time feeding and more time resting as the amount of recent rainfall increased. While the majority of these correlations does not reach statistical significance at the 0.05 level, the uniformity in the direction of the correlations suggests that most females

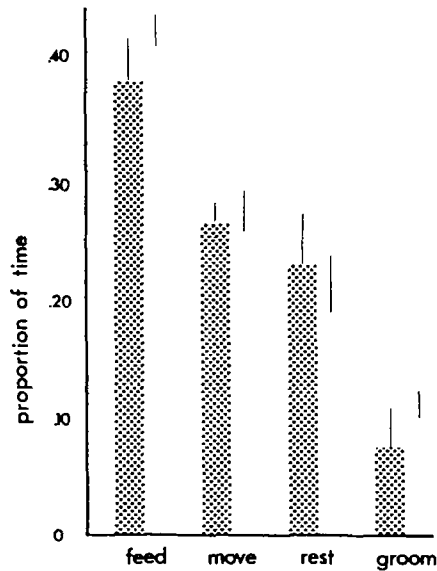


Fig. 1. Activity budgets of pregnant females. Data from observations of all females in each group that carried pregnancies to term are pooled to obtain the mean proportion of time devoted to each activity. The mean and one standard deviation from the mean are shown here. The dotted bars on the left represent Alto's Group, the stippled bars on the right represent Hook's Group.

did feed less and rest more as the amount of recent rainfall increased. The relationship between recent rainfall and the proportion of time spent grooming is less consistent; 11 of the 15 females spent more time grooming as rainfall increased. The magnitude of these correlations is consistently low. Finally, as rainfall increased seven females spent more time moving, while eight females spent less time moving.

Both changes in rainfall and changes in fetal development might have contributed to changes in females' behavior over the course of their pregnancies. However, it is difficult to tease apart the effects of these two variables upon females' behavior. Standard multiple-regression procedures are not reliable when there is collinearity among the independent variables (Wonnacott and Wonnacott, 1977). Hence, I have adopted a more conservative procedure for this analysis. A one-dimensional linear regression was fitted to the relationship between recent rainfall and the proportion of time devot-

ed to each activity. The components of the resultant regression equation were used to predict the proportion of time that females were expected to devote to each activity, given the amount of recent rainfall. Then, for each female day, the residual proportions of time spent in each activity were computed by subtracting the expected values from the observed values. The values of the residuals reflect the direction and magnitude of deviations from the expected value. A negative residual indicates that a female spent a smaller proportion of time in a given activity than was expected on the basis of the amount of recent rainfall. To analyze the pattern of change in the values of the residuals over the course of pregnancy, the residual values for each activity were regressed against gestational age.

It should be noted that analyses based upon these residuals provide quite conservative estimates of the effects of gestational age upon maternal behavior. This arises from the fact that this procedure sets aside all of the variation that is ostensibly explained by variation in rainfall, even though some of this variation may actually be due to correlated variation in gestational age. Thus, analyses based upon the untransformed data provide a maximum estimate of the effects of gestational age upon maternal behavior, while analyses based upon the residuals provide a minimum estimate of the effects of gestational age.

As their pregnancies progressed, the residual proportion of time spent grooming by pregnant females declined ($r = -0.0803$, $P = 0.051$, $N = 418$ female days in all analyses). However, the residual proportions of time spent in other activities did not change significantly (feeding— $r = 0.0553$, $P = 0.130$; resting— $r = 0.0556$, $P = 0.124$; moving— $r = -0.0130$, $P = 0.396$). When mothers of nonsurviving females were removed from the sample, the correlation between the residual proportion of time spent feeding and the gestation became significant ($r = 0.0906$, $P = 0.046$, $N = 346$ female days).

To assess the feeding behavior of individual females during their pregnancies, the regression between the gestational age and the residual proportion of time spent feeding was computed separately for each of the 15 females observed during the final two-thirds of her pregnancy. For 12 of these females, the regression slopes were positive, indicating that females spent progressively more time feeding as their pregnancies progressed. The three remaining females spent progressively less time feeding as their pregnancies progressed. This sample included two females that produced nonsurviving infants. One of these females spent progressively more time feeding as her pregnancy progressed, while the other female showed an equally strong trend in the opposite direction.

Table II. Activity Budgets of Individual Females

Female	Number of female days	Proportion of observation time spent							
		Feeding		Moving		Resting		Grooming	
		\bar{X}	SD	\bar{X}	SD	\bar{X}	SD	\bar{X}	SD
Alto's Group									
Safi	7	0.37	0.10	0.29	0.13	0.24	0.07	0.05	0.07
Fanny*	10	0.38	0.16	0.24	0.07	0.20	0.10	0.11	0.10
Eno	15	0.45	0.13	0.25	0.09	0.24	0.15	0.04	0.07
Slinky	19	0.31	0.15	0.30	0.11	0.33	0.17	0.03	0.07
Cete	19	0.41	0.13	0.30	0.11	0.18	0.12	0.09	0.09
Dotty	19	0.36	0.17	0.30	0.11	0.25	0.17	0.05	0.08
Spot	26	0.38	0.15	0.27	0.09	0.21	0.12	0.10	0.09
Oreo	25	0.42	0.14	0.26	0.12	0.25	0.13	0.04	0.07
Vee	28	0.37	0.16	0.25	0.10	0.23	0.14	0.11	0.13
Handle	20	0.44	0.10	0.27	0.07	0.15	0.09	0.12	0.10
Preg	17	0.37	0.12	0.28	0.09	0.29	0.13	0.05	0.07
Janet	17	0.38	0.12	0.28	0.12	0.24	0.13	0.08	0.10
Vixen	19	0.45	0.09	0.26	0.11	0.21	0.13	0.06	0.08
Summer	15	0.38	0.16	0.28	0.10	0.15	0.15	0.14	0.10
Nazu	10	0.53	0.14	0.27	0.10	0.09	0.05	0.09	0.11
Fanny*	10	0.44	0.15	0.27	0.10	0.18	0.12	0.05	0.03
Hook's Group									
Nubbin	14	0.38	0.15	0.23	0.08	0.24	0.14	0.07	0.08
Lamu	19	0.40	0.09	0.22	0.08	0.23	0.11	0.12	0.13
Pindua	21	0.42	0.15	0.22	0.10	0.24	0.10	0.07	0.11
Ncena	18	0.37	0.14	0.22	0.09	0.26	0.14	0.11	0.13
Moja	16	0.45	0.13	0.29	0.10	0.13	0.13	0.11	0.11
Lista	15	0.41	0.11	0.30	0.12	0.17	0.10	0.08	0.10
Penny	14	0.47	0.17	0.25	0.07	0.14	0.08	0.07	0.08
Willy	11	0.42	0.13	0.29	0.11	0.14	0.09	0.12	0.12
Kupita	6	0.40	0.09	0.29	0.10	0.14	0.06	0.15	0.12

*Fanny was pregnant twice during the study period.

Sources of Variation in Activity Patterns Among Females

The average proportion of time that females devoted to feeding, moving, resting, and grooming during their pregnancies varied among females (Table II). This variation may be due partly to the fact that focal females varied as to age, parity, dominance rank, group membership, and sex of neonates. The analysis below examines these sources of variation in activity patterns among females.

Correlations among these variables would confound this analysis. Fortunately, nearly all of these variables were independent. Members of Hook's and Alto's Group did not differ in their dominance rank ($t = -0.50$, $P = 0.622$; $N_1 = 16$ pregnancies, $N_2 = 9$ pregnancies), parities ($t = -.16$, P

= 0.873; $N_1 = 16$ pregnancies, $N_2 = 9$ pregnancies), or sex ratios of their infants ($\chi^2 = 0.618$, $P = 0.432$). Maternal parity and dominance rank were independent ($r = 0.0776$, $P = 0.356$, $N = 25$ pregnancies). Mothers of male and female infants did not differ in their parities ($t = -.068$, $P = 0.512$, $N_1 = 17$ pregnancies, $N_2 = 8$ pregnancies).

There was, however, a consistent association between maternal rank and infant sex. Mothers of females were, on average, higher ranking than mothers of males (average rank – mothers of females = 0.57, $SD = 0.308$; mothers of males = 0.31, $SD = 0.306$; $t = 1.96$, $P = 0.070$). This is consistent with earlier studies of Alto's Group which demonstrated that high-ranking females produced more daughters than sons, while low-ranking females produced more sons than daughters (J. Altmann, 1980; J. Altmann *et al.*, 1987).

Group Membership. The members of Alto's Group spent significantly more time resting (23%) than did the members of Hook's Group (19%; $t = 2.14$, $P = 0.051$, $N_1 = 16$ pregnancies, $N_2 = 9$ pregnancies in all analyses) (Fig. 1). The members of Alto's Group spent slightly less time feeding (39%) than did the members of Hook's Group (42%; $t = -1.94$, $P = 0.066$), and they also tended to spend less time grooming (8%) than the members of Hook's Group (10%; $t = -1.76$, $P = 0.093$). There were considerably fewer consistent differences in the fraction of time spent moving (Alto's Group, 27%; Hook's Group, 26%; $t = 0.88$, $P = 0.396$).

Maternal Characteristics. Maternal dominance rank had a negligible impact upon the activity budget of pregnant females. The average rank was not related consistently to the proportion of time that pregnant females spent feeding ($r = -0.1008$, $P = 0.316$, $N = 25$ pregnancies in all analyses), moving ($r = 0.2094$, $P = 0.158$), resting ($r = -0.0987$, $P = 0.319$), or grooming ($r = 0.0630$, $P = 0.382$).

Age and parity were highly correlated among females ($r = 0.9203$, $P < 0.0001$); only the relationship between parity and activity patterns is reported here, for the sake of simplicity. Multiparous (and older) females spent less time feeding ($r = -0.3321$, $P = 0.052$) and somewhat more time resting than nulliparous (and younger) females ($r = 0.3208$, $P = 0.059$). Parity had no significant effects upon the proportion of time that females spent grooming ($r = -0.1982$, $P = 0.171$) or moving ($r = 0.1864$, $P = 0.186$).

Fetal Sex. Females carrying female fetuses spent significantly more time grooming than did females carrying male fetuses (mothers of females, 9%; mothers of males, 6%; $t = 2.40$, $P = 0.033$, $N_1 = 17$ pregnancies, $N_2 = 8$ pregnancies in all analyses). However, fetal sex had little impact upon the proportion of time that females spent feeding ($t = -0.88$, $P = 0.401$), resting ($t = 0.19$, $P = 0.850$), or moving ($t = -1.49$, $P = 0.167$).

The relationship between fetal sex and the proportion of time spent grooming might be an artifact of the relationship between dominance rank and fetal sex. If so, maternal dominance rank is also expected to be related to the proportion of time pregnant females spent grooming and feeding. However, this was not the case. To distinguish between the effect of maternal rank and that of infant sex more clearly, the data would have to be partitioned by maternal rank and infant sex. For this, a considerably larger sample of pregnancies would be needed.

Feeding Behavior During Pregnancy

Baboons are omnivores. An exhaustive list of foods eaten by the Amboseli baboons numbers well over 200 items (Altmann, in preparation) and includes both plant and animal material. A much smaller number of foods are eaten regularly by the baboons, and feeding behavior varies between seasons and over years (J. Altmann, 1980; Altman, in preparation; Post, 1982; Stacey, 1986). Below, I briefly describe the foods most commonly consumed by pregnant females during my study period. The frequencies used in these analyses represent proportions of total feeding time.

The baboons fed upon various parts of many different plants (Fig. 2). A few plant parts occupied the majority of their feeding time. Females re-

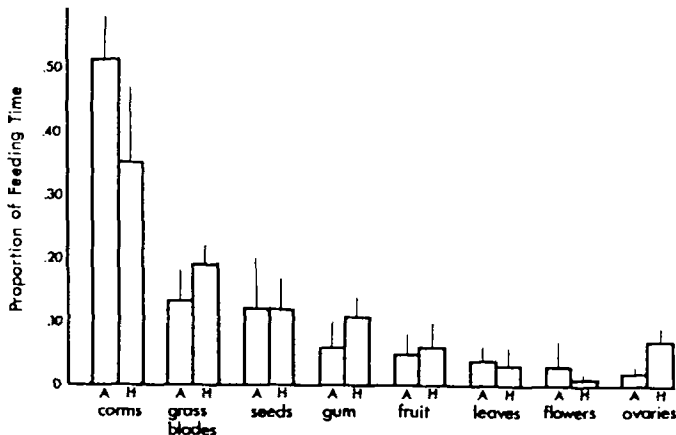


Fig. 2. Plant parts. Vertical bars indicate the proportion of total feeding time that pregnant members of Alto's Group (bars labeled A) and Hook's Group (bars labeled H) spent feeding upon different plant parts. Data from all females that carried pregnancies to term in each group are pooled to obtain the pooled mean and one standard deviation from the mean.

lied heavily upon corms, the underground storage organs of grasses and sedges. They consumed a large quantity of seeds that were extracted from the pods of the two *Acacia* species, *A. xanthophloea* and *A. tortilis*, and the pods of various small shrubs. Seeds were also obtained from the seed-heads of several grasses and were occasionally picked out of elephant and ungulate dung. *A. xanthophloea* trees provided gum, which the baboons scraped from the tree's trunk with their fingers and teeth. Baboons fed upon the flowers, leaves, and fruits of several shrubs and the two *Acacia* species. Finally, the baboons fed upon the ovaries of one plant, *Trianthema ceratosepala*.

Pregnant female baboons fed upon 45 identified plant species but relied heavily upon only a small subset of these species (Fig. 3). There were

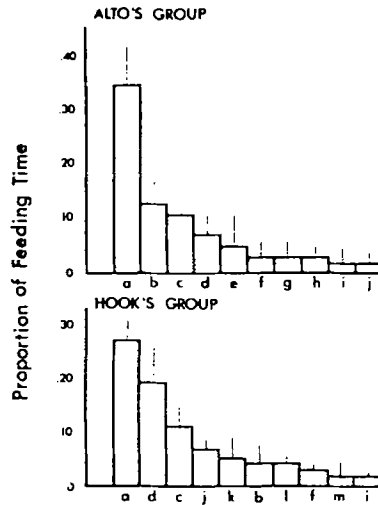


Fig. 3. Food species. The proportion of total feeding time that pregnant members of Alto's Group and Hook's Group spent feeding upon different plant species is shown here. Data from all females in each group that carried pregnancies to term are pooled to obtain the pooled mean and one standard deviation from the mean. Key to plant species: a, *Sporobolus kentrophylus*; b, *Acacia tortilis*; c, *Sporobolus cordofanus*; d, *Acacia xanthophloea*; e, *Cyperus bulbosa*; f, *Sporobolus consimilis*; g, *Azima tetracantha*; h, *Cynodon plectostachyus*; i, other grasses and sedges; j, *Trianthema ceratosepala*; k, *Withania somnifera*; l, *Cynodon nlemfuensis*; m, *Ramphicarpa montana*.

Table III. Correlates of Daily Feeding on Plant Parts and Invertebrate Prey

Food category	Correlation between proportion of total feeding time and				Correlation between residual proportion of feeding time and	
	Recent rainfall		Gestation day		Gestation day	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Corms	-0.2492	0.000	0.1078	0.014	0.0385	0.216
Seeds	-0.1824	0.000	0.2600	0.000	0.2119	0.000
Grass blades	0.3799	0.000	-0.1992	0.000	-0.0991	0.021
Leaves	0.1303	0.004	-0.0488	0.159	-0.0120	0.403
Flowers	0.2323	0.000	-0.0900	0.033	-0.0249	0.305
Fruit	-0.1035	0.017	-0.0602	0.109	-0.0900	0.033
Gum	0.0351	0.237	-0.0626	0.100	-0.0527	0.141
Plant ovaries	0.0608	0.107	-0.0730	0.068	-0.0559	0.127
Invertebrate prey	0.0642	0.095	-0.1341	0.003	-0.1162	0.009

only 10 plant species that accounted for more than 1% of the feeding time of focal females in Alto's Group and Hook's Group, although the list of these 10 species differed for members of the two groups. In both groups, the 10 major plant species constitute 84% of their total feeding time. Foods of unknown species accounted for approximately 5% of the feeding time of the members of both groups. The product of various grasses and the two *Acacia* species accounted for approximately two-thirds of the baboons' total feeding time.

Females sometimes fed upon animal matter. Vertebrate and invertebrate prey accounted for 2% of total feeding time among females in both Alto's Group and Hook's Group. Invertebrate prey included beetle larvae, caterpillars, grasshoppers, and various unidentified items. Females actively searched for invertebrate prey. They sometimes sifted through elephant dung, from which they extracted dung-beetle larvae. During the wet season they also dug for dung-beetle larvae in uninhabited Masai encampments. Feeding upon vertebrate prey was quite uncommon, but pregnant females were seen consuming bird eggs, immature birds, lizards, and immature hares during focal observations. Captures of vertebrate prey appeared to be opportunistic.

Changes in Feeding Behavior During Pregnancy

As the amount of recent rainfall increased, pregnant females consumed larger proportions of grass blades, leaves, and flowers (Table III, columns 2 and 3). At the same time, they consumed smaller proportions of grass corms, seeds, and fruit. Recent rainfall had no consistent impact upon the proportion of time spent feeding upon *Acacia* gum, plant ovaries, or invertebrate prey.

In order to determine whether the aggregate results reflected consistent changes in the feeding behavior of individual females in both groups, the correlation between recent rainfall and the proportions of total feeding time allocated to grass blades, leaves, flowers, corms, seeds, and fruit was computed separately for each of the 15 females observed during the final two-thirds of pregnancy. Most females spent less time feeding upon corms (13 of 15), seeds (11 of 15), and fruit (11 of 15) as the amount of recent rainfall increased. All females spent more time feeding upon grass blades (15 of 15) as the amount of recent rainfall increased. Two-thirds of the females spent more time feeding upon leaves (10 of 15) as a recent rainfall increased. Approximately half the females spent more time feeding upon flowers as rainfall increased (8 of 14; one female did not feed upon flowers often enough to calculate the correlation).

The feeding behavior of pregnant females also changed over the course of their pregnancies. As their fetuses matured, females devoted larger proportions of their feeding time to corms and seeds and smaller fractions of their feeding time to grass blades, flowers, invertebrate prey, and plant ovaries (Table III, columns 4 and 5). There were no significant changes in the proportion of leaves, fruit, or gum consumed as pregnancy progressed.

Since for most females the environment became drier as their pregnancies progressed, it is not surprising to find that foods frequently eaten during the wet season (such as grass blades and flowers) were less frequently eaten as their fetuses matured. To separate the effects of rainfall and consequent changes in resource availability from the correlated effects of changes in gestational age, residuals from the regression between rainfall and the proportion of time spent feeding on particular foods were computed separately for each plant part.

The residual proportion of feeding time devoted to seeds increased significantly over the course of gestation, while the residual proportion of feeding time devoted to feeding upon grass blades, fruit, and invertebrate prey declined (Table III, columns 6 and 7). There were no significant changes in the residual fraction of other foods consumed by pregnant females. Thus, as their fetuses matured, females fed upon relatively more seeds and fewer grass blades and fruits than expected on the basis of the amount of recent rainfall.

Sources of Variation in Diet

Group Membership. The members of Hook's Group and Alto's Group spent very similar proportions of their day feeding, but the frequency with which they fed upon particular foods varied considerably. Pregnant females in Alto's Group spent significantly more time feeding upon corms, and sig-

nificantly less time feeding upon grass blades, gum, and plant ovaries, than did females in Hook's Group (Table IV, columns 2 and 3). Members of both groups spent similar amounts of time feeding upon other foods.

Maternal Characteristics and Fetal Sex. Maternal age and parity, maternal dominance, and fetal sex appear to have no consistent impact upon the feeding time budget of pregnant females (Table IV, columns 4–9). While a few correlations do achieve statistical significance, the number of significant results in this group of analyses is roughly the same as one would expect by chance alone.

DISCUSSION

In this analysis, it was difficult to assess the relative importance of environmental changes and gestational age in shaping females' behavior during pregnancy, because most females conceived after the onset of heavy rains and thus experienced drier conditions as their pregnancies progressed. When rainfall was held constant in the analysis, it became evident that the behavior of most females changed as their fetuses matured. Most females spent progressively more time feeding and less time grooming than expected on the basis of the amount of recent rainfall. The fact that most females spent more time feeding as their fetuses matured is consistent with the fact that metabolic requirements rise as the fetus develops.

There were also several factors that contributed to differences in activity budgets among individuals. As parity and age increased, females fed less and rested more. This suggests that females may have alternate means of meeting their energetic requirements; while some females may increase their food intake by devoting more time to feeding, others may reduce their energy requirements by increasing the proportion of the day that they rest. It is difficult to explain why females carrying female fetuses spent more time grooming than females carrying male fetuses. The effects of fetal sex may be an artifact created by differences in maternal rank, the presence or number of kin, or the quality of social relationships among the mothers of male and female infants.

As their fetuses developed, pregnant females consumed progressively larger fractions of seeds and smaller fractions of grass blades and fruit than expected on the basis of the amount of recent rainfall. The seeds most commonly consumed by pregnant females contained more protein per unit weight than any of the other plant parts that they commonly fed upon (S. A. Altman *et al.*, 1987). The increase in the proportion of seeds consumed over the course of pregnancy may be related to the fact that protein requirements increase during the last trimester of pregnancy in humans (Hyttén, 1980).

Table IV. Correlates of Cumulative Feeding on Plant Parts and Invertebrate Prey

Food category	Group membership		Maternal rank		Maternal parity		Fetal sex	
	<i>t</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>t</i>	<i>P</i>
Corms	3.66	0.005	0.0900	0.334	-0.0579	0.392	-0.14	0.893
Seeds	-0.08	0.937	-0.2077	0.160	-0.1313	0.266	-0.16	0.877
Grass blades	-3.54	0.002	0.0292	0.445	0.0597	0.388	0.83	0.417
Leaves	0.50	0.628	-0.0130	0.457	0.3117	0.065	0.98	0.350
Flowers	1.70	0.107	0.0880	0.338	-0.0736	0.363	0.18	0.860
Fruit	-0.79	0.446	0.1072	0.305	-0.2371	0.127	-1.23	0.232
Gum	-3.37	0.003	-0.2476	0.116	0.0774	0.357	0.09	0.930
Plant ovaries	-6.03	0.000	0.1332	0.263	-0.1490	0.239	-0.96	0.353
Invertebrate prey	-0.26	0.802	-0.1273	0.272	0.0405	0.424	-0.48	0.639

Despite this, some valuable potential sources of protein were exploited less frequently than expected as pregnancy progressed. Females spent significantly less time than expected feeding upon and searching for invertebrate prey as their fetuses matured. Although invertebrate prey were good sources of protein, they may have been costly or difficult for pregnant females to obtain. In December and January, females ate small caterpillars that they plucked from the terminal ends of grass shoots. These caterpillars were abundant in the grasses of the plains and required little effort to obtain. The availability of caterpillars declined, and during the dry season invertebrate prey consisted mainly of beetle larvae found in elephant dung and winged grasshoppers trapped on the ground or caught in flight. These prey seemed to be considerably more difficult to obtain. Beetle larvae were patchily distributed and the object of considerable competition. Winged insects were not encountered often and required considerable agility and effort to catch. Pregnant females may have concentrated their efforts upon obtaining foods that were more accessible.

Females conceived after months of heavy rain when food was relatively abundant. During their pregnancies, conditions deteriorated considerably. Despite this, most pregnancies were successful; 22 of the 27 conceptions (81%) detected resulted in surviving infants, and 22 of the 25 (88%) infants that were carried to term were viable. Females seem to have coped with the deterioration of environmental conditions over the course of their pregnancies in several different ways. First, they adjusted their activity budgets; the proportion of time spent feeding increased, and the proportion of time spent socializing decreased. Second, their feeding behavior changed; they increased their consumption of accessible high-protein items. Finally, pregnancy may have been prolonged. Females whose pregnancies ended during dry periods were pregnant significantly longer than females whose pregnancies ended during wetter periods (Silk, 1986).

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REFERENCES

- Altmann, J. (1974). Observational study of behaviour: Sampling methods. *Behaviour* 44: 227-267.
- Altmann, J. (1980). *Baboon Mothers and Infants*, Harvard University Press, Cambridge, Mass.
- Altmann, J. (1983). Costs of reproduction in baboons (*Papio cynocephalus*). In Aspey, W. P., and Lustick, S. I. (eds.), *Behavioral Energetics: The Cost of Survival in Vertebrates*, Ohio State University Press, Columbus, pp. 67-68.
- Altmann, J., Altmann, S. A., and Hausfater, G. (1987). Determinants of reproductive success in savannah baboons (*Papio cynocephalus*). In Clutton-Brock, T. H. (ed.), *Reproductive Success*, University of Chicago Press, Chicago (in press).
- Altmann, S. A., and Altmann, J. (1970). *Baboon Ecology*, University of Chicago Press, Chicago.
- Altmann, S. A., Post, D. G., and Klein, D. F. (1987). Nutrients and toxins of plants in Amboseli, Kenya. *J. Afr. Ecol.* (in press).
- Cheek, D. B., Holt, A. B., London, W. T., Ellenbery, J. A., Hill, D. E., and Sever, J. L. (1976). Nutritional studies in the pregnant rhesus monkey—the effect of protein-calorie or protein deprivation on growth of the fetal brain. *Am. J. clin. Nutr.* 29: 1149-1157.
- Coelho, A. M., Glassman, D. M., and Bramblett, C. A. (1984). Relation of adiposity and body size to chronological age in olive baboons. *Growth* 48: 445-454.
- Collins, D. A. (1984). Spatial pattern in a troop of yellow baboons (*Papio cynocephalus*) in Tanzania. *Anim. Behav.* 32: 536-553.
- DiGiacomo, R. F., Shaughnessy, P. W., and Tomlin, S. J. (1978). Fetal-placental weight relationships in the rhesus (*Macaca mulatta*). *Biol. Reprod.* 18: 749-753.
- Hausfater, G. (1975). Dominance and reproduction in baboons (*Papio cynocephalus*). *Contrib. Primatol.* 7: 1-150.
- Hytten, F. E. (1980). Nutrition. Weight gain in pregnancy. In Hytten, F. E., and Chamberlain, G. (eds.), *Clinical Psychology in Obstetrics*, Blackwell Scientific Publishers, Oxford, pp. 163-223.
- Kohrs, M. B., Harper, A. E., and Kerr, G. R. (1976). Effects of a low-protein diet during pregnancy of the rhesus monkey I. Reproductive efficiency. *Am. J. clin. Nutr.* 29: 136-145.
- Lancaster, J. (1984). Evolutionary perspectives on sex differences in the higher primates. In Rossi, A. (ed.), *Gender and the Life Course*, Aldine, New York, pp. 3-27.
- Leutenegger, W. (1973). Maternal-fetal weight relationship in primates. *Folia primatol.* 20: 280-293.
- Nicolson, N. (1982). *Weaning and the Development of Independence in Olive Baboons*, Ph.D. dissertation, Harvard University, Cambridge, Mass.
- Portman, O. W. (1970). *Nutrient Requirements of Monkeys*, National Academy of Sciences-National Research Council Publication 990, Washington, D.C.
- Portman, O. W., Alexander, M., Neuringer, M., Novy, M., Illingworth, R., and Uno, H. (1977). Effects of perinatal malnutrition on lipid composition of neural tissues from rhesus monkeys. *J. Nutr.* 107: 2228-2235.
- Post, D. G. (1982). Feeding behavior of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya. *Int. J. Primatol.* 3: 403-430.
- Post, D. G., Hausfater, G., and McCuskey, S. A. (1980). Feeding behaviour of yellow baboons (*Papio cynocephalus*): Relationships to age, gender, and dominance rank. *Folia primatol.* 34: 170-195.
- Ransom, T. W., and Rowell, T. E. (1972). Early social development in feral baboons. In Poirier, F. (ed.), *Primate Socialization*, Random House, New York, pp. 105-144.
- Riopelle, A. J. (1982). Protein deprivation and offspring behavior. In Fitzgerald, H. E., Mullins, J. A., and Gage, P. (eds.), *Studies of Development in Nonhuman Primates. Vol. 3: Child Nurturance*, Plenum, New York, pp. 3-24.

- Riopelle, A. J., and Shell, W. F. (1978). Protein deprivation in primates. XI. Determinants of weight change during and after pregnancy. *Am. J. clin. Nutr.* 31: 394-400.
- Saayman, G. S. (1972). Aggressive behaviors in free-ranging chacma baboons. *J. behav. Sci.* 1: 77-83.
- Sackett, G. P., Holm, R. A., Davis, A. E., and Fahrenbruch, C. E. (1975). Prematurity and low birth weight in pigtail macaques: Incidence, prediction, and effects on infant development. In Kondo, S., Kawai, M., Ehara, A., and Kawamura, S. (eds.), *Proceedings from the Fifth Congress of the International Primatological Society*, Japan Science Press, Tokyo, pp. 189-206.
- Samuels, A., Silk, J. B., and Altmann, J. (1987). Consistency and change in dominance relationships among female baboons. *Anim. Behav.* 35: 785-793.
- Silk, J. B. (1986). Correlates of variation in gestation length in free-ranging baboons (*Papio cynocephalus*). *Int. J. Primatol.* 7: 583-602.
- Snow, C. C. (1977). *The Physical Growth and Development of the Open-Land Baboon, Papio doguera*. Ph.D. dissertation, University of Arizona, Tucson.
- Stacey, P. B. (1986). Group size and foraging efficiency in yellow baboons. *Behav. Ecol. Sociobiol.* 18: 175-187.
- Strum, S. C., and Western, D. (1982). Variations in fecundity with age and environment in olive baboons (*Papio anubis*). *Am. J. Primatol.* 5: 93-109.
- Tanner, J. M. (1970). *Growth at Adolescence*, Blackwell, Oxford.
- Walters, J. (1980). Interventions and the development of dominance relationships in female baboons. *Folia primatol.* 34: 61-89.
- Whitten, P. L. (1983). Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *Am. J. Primatol.* 5: 139-159.
- Whitten, P. L., and Smith, E. O. (1984). Female rank and food intake in captive stump-tail macaques (*Macaca arctoides*). *Am. J. phys. Anthropol.* 6: 426.
- Wonnacott, T. H., and Wonnacott, R. J. (1977). *Introductory Statistics*, John Wiley and Sons, New York.
- Wrangham, R. W. (1981). Drinking competition in vervet monkeys. *Anim. Behav.* 29: 904-910.