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## Costs of maternal care: infant-carrying in baboons

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**Summary.** Infant-carrying, the most costly form of primate parental care other than lactation, was investigated in savannah baboons of Amboseli, Kenya. Measurements of physical growth, counts and length of paces, and simultaneous records of carrying and locomotion were used to evaluate the time, distance, and energetic expenditure of infant-carrying. Finally, we modeled the energetics of independent infant locomotion and considered ontogenetic patterns in the alternative energetic costs of carrying versus independent infant locomotion under assumptions of complete nutritional dependency. The youngest infants were carried by their mothers during all travel and foraging, for a total of 8–10 km/day. By 8 months of age, both carrying time and distance were almost zero. However, daily carrying distance, unlike carrying time, did not decline in the first few months, because older infants were carried disproportionately during rapid travel and, consequently, for greater travel distances per unit carrying time. Females of low dominance rank carried their infants the most; the highest ranking mothers not only carried their infants least but biased their carrying against sons. Although carrying a growing infant is an increasingly costly behavior, during the period of nutritional dependence energetic costs to the mother are appreciably greater if an infant travels independently instead of being carried by its mother. Yet infants increased locomotor independence at a younger age than predicted by a simple model of maternal energetic efficiency. Trade-offs in energetic economy may enhance a mother's future reproduction at the expense of her present infant, may enhance survival of the present infant by promoting early acquisition of developmentally essential skills, or may suggest the importance of additional factors that influence the mother's and infant's behavior.

### Introduction

Animals allocate resources, both time and energy, to offspring care at a cost to their own maintenance, survival, or future reproduction. For female mammals, lactation is the form of post-natal care that has been investigated most thoroughly, from proximal physiological and behavioral perspectives through ones that are ecological and evolutionary. Infant-carrying has received much less attention, although among forms of parental care its potential costs are second only to lactation for mammals whose young are neither precocial in locomotion nor “parked” in nests or caches. The demands of carrying are especially great for non-sedentary species that travel long distances on a daily basis in order to forage. The combined stresses of lactation and carrying may be even greater than they first appear if providing such care not only is costly of time and energy but also reduces the efficiency of parental foraging, predator avoidance, or other essential activities. As infants mature and can locomote independently while still completely nutritionally dependent on their mothers, independent locomotion by infants provides an alternative to carrying, but one that potentially requires even greater levels of lactation.

The present study was undertaken to identify the costs in time and energy of infant-carrying among wild-living primates, to evaluate sources of variability in this form of parental investment, including predicted potential differentials in cost or benefit based on dominance rank, offspring sex, or ecological conditions, and to consider consequences of independent offspring locomotion as an alternative to carrying. The research was conducted on yellow baboons, *Papio cynocephalus*, in Amboseli National Park of southern Kenya. Baboons are among the largest, most sexually dimorphic, and most terrestrial of the monkeys (Rowell 1964; Stoltz and Saayman 1970). They live in semi-closed matrilineal social groups consisting of males and females of all ages. Baboons are omnivores that, in their savannah habitats,

forage long distances each day and often use different sleeping sites on consecutive nights (Altmann and Altmann 1970, Hamilton 1982; Hausfater and Meade 1982). Detection of and protection from predators is such an important benefit of group living for these animals ( DeVore and Hall 1965; Altmann and Altmann 1970) that individuals make extreme efforts to keep up with their group, even a few minutes or hours after parturition (Altmann 1980) or when slowed by illness or aging.

Like most anthropoid primates, baboons produce a single infant with each gestation. A newborn baboon weighs a little less than 1 kg, approximately 7% of its mother's body mass. At birth, a neonate is carried continuously as it clings to its mother's ventrum, grasping with hands and feet to the fur on her sides. After a few months, the infant generally shifts to sitting or lying on its mother's back (DeVore 1963; Ransom and Rowell 1972; Rasmussen 1979; Altmann et al. 1981; Rhine et al. 1984). Infant-carrying by individuals other than the mother is rare and usually of brief duration. As the infant grows, at a rate of 4–5 g/day for savannah baboons (Altmann 1980; Nicolson 1982; Altmann and Alberts 1987; Eley et al. 1989), the energetic costs of maintenance, growth, and transport increase. At the same time, however, the infant gradually improves in its ability to provide some of these forms of care for itself. As the maturing infant's needs and abilities change, so does its mother's ability to provide for herself, for this current infant, and for her own future reproduction (Altmann 1983).

Most maternal care declines after the infant is several months old (DeVore 1963; Ransom and Rowell 1972; Nash 1978; Altmann 1980; Nicolson 1982, 1987; Rhine et al. 1984, 1985). Although some amount of suckling, thermoregulatory and predator protection, and social support continues beyond the first year of life, mothers in two groups of Amboseli baboons usually resume sexual cycling by the time their infants are 8–14 months of age, and conception occurs a few months later. Inter-birth intervals, consequently, are a little under 2 years (Altmann et al. 1977, 1981; see also similar values for anubis baboons in Gilgil, Kenya: Nicolson 1982; Strum and Western 1982; Smuts and Nicolson 1990; and for hamadryas baboons in Ethiopia: Sigg et al. 1982). In Amboseli, infant-carrying and daytime suckling are seen infrequently beyond the second trimester of the mother's next pregnancy, usually terminating in the first half of the infant's second year of life.

Although the general form and time scale of suckling and carrying have been reported for many primate species, few quantitative data are available on these variables or on the sources or magnitude of within- or between-group variance in any form of care. The few published reports are based almost entirely on the time spent in care (e.g., Altmann 1980; Nicolson 1982; Rhine et al. 1984, 1985; Johnson 1986) rather than on measures that might better reflect energetic or life history costs. The relationship of time investment in care to the energetics of that care has remained unexplored for any form of post-natal care in non-human primates. Major sources

of variance were expected to include differences in habitat quality and its changes, offspring sex, and differential social stressors and feeding interruptions that are related to dominance rank; consequently, each of these was incorporated into the design of the project. The present study is part of a series of investigations into the sources of variance in parental care and offspring development, both their causes and their life history consequences.

## Subjects and methods

The subjects of this study were the 30 mother-infant pairs in two baboon groups, Alto's and Hook's, whose home ranges include Amboseli National Park of southern Kenya. All members of these groups are identified by individual physical characteristics and have been part of longitudinal research projects, those in Alto's since 1971, in Hook's since 1980. The histories of most of these mothers are known at least since menarche, and many have been studied since their own birth. Hook's Group lives in a habitat that is adjacent to, though slightly better than, that of Alto's; waterholes are more abundant and dry-season foods more varied (Altmann et al., unpublished).

### Data collection

*Overview.* To answer our questions about infant-carrying and the energetic cost incurred by a mother in providing such care, we needed to identify which factors determine when a mother carries her infant, how much carrying she does, and the energetic cost of that carrying. Data were collected during each behavior sample on time spent in carrying and were then associated with demographic, sociological, and ecological information. We were convinced, however, that "time spent traveling," an easily obtainable measure, would not provide an adequate estimate of the speed or distance traveled. Consequently, we obtained measurements to estimate each mother's mean pace length, and in a subset of behavioral samples, we simultaneously recorded both the number of paces the mother took and the time she spent traveling. These data were used for calibration purposes to estimate distance traveled in the larger body of data. Cross-sectional data on body mass of infants (Altmann and Alberts 1987) were used to estimate the average body mass of infants of each age for the present analyses. In more detail, the several different kinds of data sets used in these analyses are as follows:

*Infant age.* Infant age was calculated from birthdates that are known within a few days, and usually to the day, using census and neonatal assessment records (Altmann and Altmann 1970; Altmann 1980).

*Maternal dominance rank.* To evaluate effects of social stressors on maternal behavior (Altmann 1980), outcomes of "decided" agonistic bouts (Hausfater 1975; Hausfater et al. 1982), collected daily on an ad libitum basis, were used to determine a mother's dominance rank when her infant was born.

*Season.* During the dry season, food and water are less available and the baboons devote more time to traveling and feeding. We categorized each month as "wet" or "dry" by using a mean daily rainfall of 0.02 cm as the cutoff; monthly rainfall in Amboseli is bimodally distributed and values were seldom close to the cutoff.

*Pace length.* We determined the mean pace length for each mother through measurements made when she was traveling on flat ground at a walking gait in an essentially straight path. For each sample one observer marked as the starting point the placement of the heel of the mother's left foot; the second observer noted the starting

time and counted each subsequent placement of the left heel (equal to one pace) until the female had taken at least 10 but usually 20 paces. The ending time was recorded, the ending point marked, and the distance traversed was measured. For each sample, mean pace length was obtained by dividing the distance traveled by the number of paces. Pace rate, the number of paces per second, was calculated to determine whether pace length within the range of walking speeds was a function of speed. Average values for pace length varied little with speed over a range of 0.7 to 1.4 paces per second ( $N=294$  pace-length samples). We obtained 10 of these samples for almost every female, and sample means for each female were averaged to obtain individual-specific values for pace length.

**Behavioral data.** For several different projects, focal (continuous) sampling (Altmann 1974) of the behavior of mothers was conducted throughout the 17-month period in 1983 and 1984. Subsets of the data collected during each of these projects could be used in the present analyses ( $N=2390$  samples). Sample durations were either 10 or 20 min, depending on the project. Three mothers, selected for proximity of their infants' ages, were observed on a given day. We rotated sampling among the three focal females of the day during each hour from 0740 through 1700, with the exception of 1200, for a maximum number of eight 10-min samples or four 20-min samples per female per day.

Each behavioral sample was labeled with the date, hour of the day, infant age and sex, maternal dominance rank, group membership, and an estimated group- and age-specific value for infant body mass. Behavioral data included time spent in various activity states and in mother-infant interactions. The states of interest for the present analyses were "infant-carrying" by the mother, defined as supporting the entire weight of her infant while standing or locomoting, and "traveling" by the mother, defined as locomotion while not ingesting food. Although our definition of traveling includes running and climbing, virtually all of the baboons' travel in Amboseli is terrestrial and at a walking gait. Infant-carrying data were also derived from a separate set of 20-min samples ( $N=517$ ) in which the infant was the focal subject.

The data were collected with a MORE electronic event recorder (Observational Systems, Seattle) with a built-in clock. Elapsed time within a sample was associated with each scored behavioral transition.

A subset ( $N=491$ ) of the 10-min behavioral samples was designated ahead of time as pace-counting samples. In these samples, we recorded onset and termination of infant-carrying and other activity states while we simultaneously recorded each pace taken by the female, even paces taken while feeding or engaged in other activities. Subjects for pace-counting samples were mothers of infants aged 3–9 months. This type of sampling was sufficiently intensive to preclude the recording of most social interactions and could not be maintained beyond a 10-min period. By using pace-counting samples to evaluate the relationship between distance traversed and time spent traveling, we could then convert the time spent traveling in non-pace-counting samples into an estimate of actual distance traversed.

For purposes of analysis, values for time spent traveling, time spent infant-carrying, and distance traveled were divided by insight sample time, obtaining "proportion of time" and "speed," respectively.

**Body mass.** In a separate project (Altmann and Alberts 1987), we obtained body-mass data for immature animals of these two baboon groups. Group-specific regression lines of body mass against age were calculated from those data and used to estimate the body mass of an infant on the date of each behavioral sample.

## Data analysis

**Time spent carrying.** The factors that best account for between-sample variability in the proportion of time that a mother carried

her infant were determined by using GLM (general linear model) procedures in SAS (SAS Institute, 1985) on the data points from each behavioral sample. Group membership, sex of infant, age of infant, maternal dominance rank, season, time of day, and estimated speed of travel (distance traversed per unit of observation time) were considered as independent variables predicting infant-carrying as the dependent variable. Next, for each infant and each "month" of age (actually 28-day age block), the median proportion of time spent being carried in all samples was calculated, and the GLM procedures were used to predict age-specific values. In each case, the final model retained and ordered variables by their contribution to explained variance. No improvement in adherence to model assumptions or in predictive ability was achieved by data transformation in either case, and we consequently used the untransformed data.

The multivariate results are given below. In addition, for illustrative purposes, we include several plots using single independent variables and one using two independent variables. The multivariate analyses of necessity raise questions regarding sample independence and potential problems resulting from unequal sample sizes. Consequently, we examined each multivariate finding for consistency within subsets (e.g., whether group differences were consistent across dominance ranks or within each sex). We place confidence only in those findings that are highly significant by conventional standards and/or are consistent across subsets, although we provide for the reader probability levels in each case and we indicate any departure from consistency across subsets.

**Distance traveled.** Pace-counting samples were analyzed first to estimate the distance traversed in that subset of samples and to establish the relationship between the proportion of time spent traveling and the total distance traversed during a sample. Distance traversed during a sample was estimated as the number of paces taken multiplied by that mother's average pace length. For each hour of the day and each group of baboons, we then calculated the least-squares regression of distance traversed by the mothers against the amount of time they spent traveling, and we tested these for equality of regression slopes.

The regression slopes for hours of the day were significantly different from one another. However, for only 1 h of the day was there a significant difference in values for the two baboon groups, and the direction of difference between groups was not consistent across hours (see Altmann and Samuels, in preparation, for details of quantitative results).

Consequently, in the larger data set in which we did not count paces, time spent traveling was multiplied by hour-specific but not group-specific regression slopes to estimate distance traversed in each sample. We were thereby able to obtain for non-pace-counting samples an estimate of distance traversed that was much better than if we had used only the proportion of time spent traveling, though not quite as good as if we had been able to count the exact number of paces or to measure directly the distance traversed.

To calculate distance traveled during an entire day, travel during the time for which we do not have data but during which the animals are active, 1200 and 1700 h, were assumed to be the same as the average for all the other daytime hours.

**Distance infants were carried.** Because time spent carrying and time spent in a quadrupedal posture are virtually identical for mothers of 1- and 2-month olds, the average time spent in a quadrupedal posture at each speed was estimated by the carrying time at that speed for mothers of very young infants. The distance that an infant of any age was carried during a sample was then calculated on the assumption that the ratio of carrying distance to travel distance at each speed was the same as the ratio of the time spent carrying to the time spent in quadrupedal posture when a female traveled at that speed.

**Energetics.** Finally, we estimated daily energetic expenditure for mothers of nutritionally dependent infants of various ages that

either locomoted independently or, alternatively, were carried by their mothers. For energetic costs of each individual's own independent locomotion, we of necessity assumed that the documented cross-species allometric relationships for energetics of locomotion also apply within a species, and particularly that they apply ontogenetically (see Gould 1975 for caveats), and we use the allometric exponents for energetic expenditure for primates tabulated in Taylor et al. (1982, Table 2).

Energetic equations usually are presented in terms of oxygen consumption and then converted to energetic expenditure; assuming that anaerobic metabolism is negligible (Taylor et al. 1982, p. 1), we used the energetic equivalent of 1 ml O<sub>2</sub> is 20.1 kJ. Although oxygen consumption per unit of body mass is a non-linear function of total body mass, it is a linear function of speed (Taylor et al. 1982, eq. 6). To calculate total body energetic expenditure at a given speed, rather than mass-specific expenditure, we multiply through by the body mass,  $M_b$ , and use the mammalian-order-specific values for the slopes and intercepts: coefficients of 0.523 and 0.345 and exponents of  $-0.298$  and  $-0.157$  (for the slope and Y-intercept, respectively) for primates (Taylor et al. 1982; Table 2). The resulting equation for  $E$ , the energetic expenditure, in kJ/km, as a function of body mass,  $M_b$ , is:

$$E = (20.1)((0.523)M_b^{(1-0.298)}) + (0.345 M_b^{(1-0.157)})$$

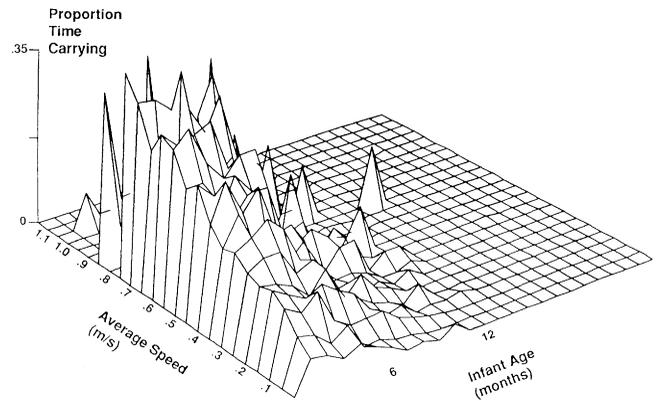
Values were calculated in this way for daily energetic expenditure during time spent at each travel speed. The need to calculate these values separately for different travel speeds results from the following problem: although energetic expenditure while walking is linear with speed, the Y-intercept is appreciably above resting values of energetic expenditure (the "Y-intercept problem"; see, e.g., Herreid and Full 1988 for a review and discussion). Because much of baboons' locomotion is of a start-and-stop sort, particularly during foraging, the influence of the high Y-intercept is considerable. Using intervals of travel speed of 0.05 m/s and the time and distance traversed for each sample, we estimated the daily distance, in km, that females traversed at each speed during the 11 h of active time. Then we calculated, for each speed, the energetic expenditure per day for the distance that was spent in locomotion at that speed.

Total daily daytime energetic expenditure was then calculated as an expected value,  $[\sum x f(x)]$ , i.e.,  $[\sum \text{prob}(\text{speed}) (\text{energetic cost at that speed})]$ , summing over all speeds of travel during a day; the probability of travel at each speed was estimated by the proportion of time spent at that speed. The daily total was calculated for a mother traveling on her own and for an infant traveling on its own under the assumption that an infant could and would walk alongside its mother. We then calculated incremental expenditure for infant-carrying, beyond that of the mother's own locomotion, using the ratio of the infant's weight to the mother's weight, using the results in Taylor et al. (1980). Basal values were assumed to apply for energetic expenditure during the 13 non-daytime h.

## Results

### *Sources of variability in time spent carrying an infant*

The faster a mother traveled, the greater the proportion of time that she carried her infant (Fig. 1) during that travel. Second, the proportion of time that the infant was carried decreased steadily as the infant became older (Fig. 1). However, older infants were not just carried for less time. With age, infant-carrying dropped out disproportionately at slow speeds and was maintained disproportionately during the most rapid travel (Fig. 1). Consequently, older infants were carried for greater distances than would be inferred solely from time spent carrying. A mother's speed of travel and her infant's



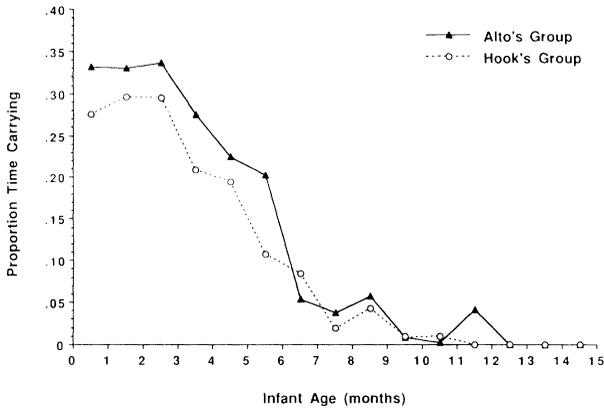
**Fig. 1.** Sources of variability in the proportion of time infants were carried: infant age and mother's travel speed (model  $r^2 = 0.45$ ,  $P < 0.0001$ )

age were the two best predictors of the proportion of time within a sample that a mother carried her infant; these two variables jointly accounted for 45% of the sample-to-sample variance in infant-carrying time ( $P < 0.0001$ ).

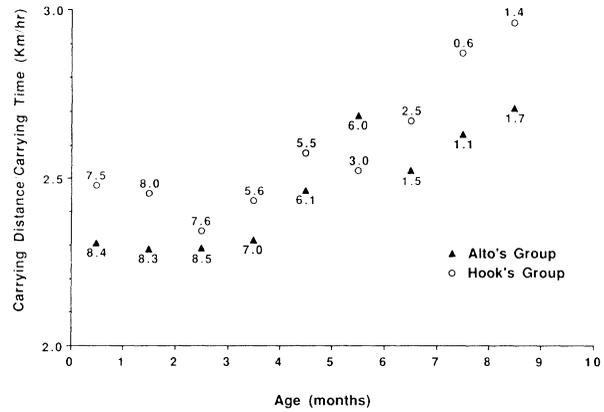
Neither season nor hour of the day significantly or consistently affected the likelihood that a mother would carry her infant ( $P > 0.05$  in each case), aside from effects accounted for by differences in speed of travel at different times of day.

The patterns of variability were examined further by calculating the median values of infant-carrying time for each infant for each month of age (28-day block). The mother's speed of travel was no longer a relevant independent variable in these analyses because mean speed of travel by mothers did not vary significantly by month of infant age. Consequently, these analyses could make use of behavioral samples taken with the infant as the focal individual in addition to those in which the mother was the focal subject. As expected, age was the best predictor of the average amount of time an infant was carried during a month ( $P < 0.0001$ ). Neonates were carried continuously, and by 8 months of age infants were very rarely carried.

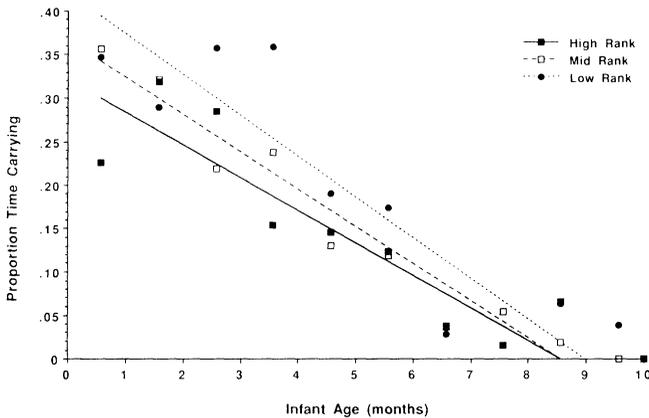
Infants of Alto's Group were consistently carried for more time per day than were Hook's Group infants of the same age, both on a sample-to-sample basis ( $P < 0.0001$ ) and in monthly averages (Fig. 2,  $P < 0.002$ ). Mothers did not consistently carry either male or female infants preferentially ( $P > 0.05$  in the sample-by-sample analyses,  $P > 0.05$  in the monthly analyses), and there was not even a trend in the monthly analyses when sex of infant alone was the only variable considered ( $P > 0.65$ ). At both levels of analysis, low-ranking females (ranks 14–21) tended to carry their infants more than did mid-ranking ones (ranks 8–13), that, in turn, carried more than did high-ranking females (ranks 1–7; see Fig. 3;  $P < 0.01$ ). This difference is clear only for male infants; low-ranking females carried infants the most, daughters almost as much as sons, and females of increasingly higher rank not only carried their infants less but also biased their infant-carrying against sons. However, the tendency for mothers of Hook's Group to pro-



**Fig. 2.** Sources of variability in the proportion of time infants were carried: bivariate plot of differences by group membership (see text for details)



**Fig. 4.** Age changes in the relationship between carrying time and distance that infants are carried per hour of carrying time: means for infants of each group at each age. Numbers adjacent to plotted points indicate the mean daily distance infants of that age were carried



**Fig. 3.** Sources of variability in the proportion of time infants were carried: bivariate plot of points and regression lines by maternal dominance rank (see text for details)

duce a higher proportion of female infants than do the mothers of Alto's Group (Altmann, unpublished data), and the tendency in both groups for high-ranking females to produce relatively greater proportions of female infants than do low-ranking females (Altmann 1980; Altmann et al. 1988 for Alto's Group; Altmann, unpublished data for Hook's Group), make it difficult to tease apart the effects of maternal rank and infant gender at this time.

*Relationship between the time and the distance that infants are carried*

Our estimates of daily travel distance for the females of this study, unlike previous estimates for this population (Altmann and Altmann 1970, Post 1978, Altmann 1980), were based on the actual paces taken by females and thus include even local travel, during all activities, that would not show up on the scale of our day-journey maps. Not surprisingly, our present procedure resulted

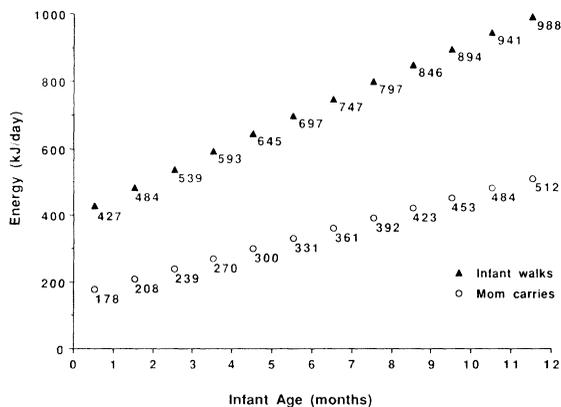
in a larger and more realistic value (cf. S. Altmann 1987); the mothers in this study traveled 8–10 km/day.

How did these long travel distances and variability in travel speeds affect infant-carrying? Although time a mother spent in infant-carrying declined rapidly after an infant was 3 months old, the distance that a mother carried her infant did not. Figure 4 shows both the mean daily distance infants were carried per unit carrying time at each age and, for comparison, the total distance per day that infants of that age were carried (data from all infants pooled within groups). The fact that, on average, a mother increasingly carried her infant at greater distances per unit of carrying time, i.e., at greater speeds, at first compensated for most of the decrease in carrying time. By 4 months of age in Hook's Group and by 5 in Alto's, however, the decrease in carrying time overwhelmed the increase in average speed during carrying, and by 8 months of age infants were rarely carried at any speed of travel.

*Energetic expenditure: maintenance, growth, and infant-carrying versus independent infant locomotion*

We calculated estimated daily energetic expenditure by females independent of reproduction or infant care. We then estimated maintenance energetic requirements for infants at various ages. Our estimates were first based on the assumption that all of an infant's travel was through being carried by its mother and then based on the assumption that the infant walked alongside its mother. Finally, we calculated the additional daily energetic cost required for infant growth. Given the patterns of locomotion observed in this study, an 11-kg adult female would expend 3493.7 kJ/24 h just for her own maintenance, i.e., exclusive of reproduction or infant care (see Methods for details of calculations).

Mothers with young infants have additional energetic requirements to support both the growth and the maintenance of their infants. At 21 kJ/g for the production of new tissue (Paine and Waterlow 1971), Amboseli in-



**Fig. 5.** Additional energetic expenditure for transportation of a nutritionally-dependent infant under two different scenarios: if the mother provided all transport by carrying the infant or, alternatively, if the infant provided all transport by walking on its own (see text for further explanation)

fants that gain 4–5 g/day (Altmann and Alberts 1987) require approximately an additional 100 kJ/day for growth. In addition to supporting her infant's growth, however, a mother that is providing all of her infant's nutritional requirements through lactation would require an additional 5% (178 kJ/day) to maintain her 0.71 kg neonate during its first month of life if she provided all its transportation through carrying, 12% (427 kJ) if the infant (somehow) walked along beside her (Fig. 5). During the next half year of an infant's life, the daily energetic costs for maintenance and activity (but not production of new tissue) incurred by the increasingly larger infant doubles (361 kJ vs 178 kJ) if the infant were to be carried all the time and nearly doubles (747 kJ vs 427 kJ) if the infant were to walk but were still dependent on its mother for nutrition. Although the absolute difference between carrying and independent locomotion increases slightly as the infant ages, the relative cost of independent locomotion decreases but averages approximately double the value for carrying throughout this age span.

The extra costs of infant maintenance and growth must be met either by the mother, through lactation, or by the infant, through independent feeding. If a mother were to provide, through lactation, all of her 7-month-old's energetic needs, including both growth and maintenance, she would require almost 15% more than her own needs if the infant were carried, almost 25% if her infant walked on its own, and even more if we included the rapid, often erratic and less linear locomotion of infants rather than the relatively conservative adult walking that we assumed in the present calculations.

## Discussion

During the first 2 months of her infant's life, a baboon mother carries her infant wherever she goes. With increasing age, the infant sits beside her or moves along with her during some of the time she spends standing

or moving very slowly. Because the infant is still carried when its mother moves at any more rapid pace, the 3-month-old infant continues to ride for much of the distance that its mother travels during the day. The cost of transport increases, however; at a 4–5 g/day growth rate, a baboon infant in Amboseli doubles its birth weight during its first 5 months of life. The infant's energetic requirements for growth, transportation, and maintenance all increase. Until an infant can feed independently, these costs are met entirely by a mother through lactation, whether she carries the infant or provides even more energy for the infant to walk on its own.

Because the distance that an infant was carried did not decrease for several months in the present study, an infant's increasing size would result in an increase in its mother's actual energetic expenditure for the infant's maintenance during this period of complete nutritional dependence. After several months without significant decline, the distance infants were carried dropped precipitously; this sharp change in the time course of distance and energetics of carrying is in contrast to time spent in carrying, contact, and suckling, all of which are described by more gradual and monotonically decreasing functions. By 6 months of age in Hook's group and 7 in Alto's group, however, even carrying time dropped appreciably (Fig. 2; see also Rhine et al. 1984, 1985; Johnson 1986). By the time an infant of either group was 8 months old, it provided virtually all of its own locomotor transport except during extremely rapid travel and during flight from external threats such as predator attacks. When translated into energetic expenditure, group differences in carrying time would be counteracted by slightly different patterns of travel (unpublished) and by differences in growth rates between the groups (Altmann and Alberts 1987). Nonetheless, residual daily energetic advantage to mothers in Hook's group would be cumulative over the period of maternal care, and if energy is a limiting factor for reproduction in Amboseli, this disparity could result in a non-negligible difference in cost of parental investment that warrants future attention.

Low-ranking females tended to carry their young infants more than did high-ranking ones and, among high-ranking females, mothers tended to carry daughters more than sons (Fig. 3). This behavioral differential is consonant with, and may contribute to, the sex- and rank-related patterns of infant mortality we have found in Alto's Group (Altmann et al. 1988); these together suggest potentially complex patterns of differential parental investment.

All other things being equal, a mother would save energy if she carried her infant rather than allowed it to locomote independently while the infant is still completely nutritionally dependent (Fig. 5). The efficiency of carrying versus independent infant locomotion results only partially from the energetics of allometry and of carrying (reviewed in Taylor et al. 1980, 1982), which we included in our calculations. An even larger and more realistic differential would result if we could incorporate the fact that infant baboons, when moving on their own, are more active than their mothers, take more circuitous

routes, and thus walk farther and expend even more energy.

Despite these advantages of carrying, several factors probably tip the balance in favor of increased locomotor independence for a 4-month-old infant. The most immediate factors are probably the infant's large size and high levels of activity, which increasingly result in interference with its mother's feeding activity (Altmann 1980; Whitten 1982; Johnson 1986). For vervet monkeys, Whitten (1982) found that a mother's feeding was less efficient when her infant was in contact, even during the infant's first months of life. Second, a 4-month-old baboon infant may be able to provide some of its own nutrition (Dunbar and Dunbar 1988). Time that the infant is off its mother during slow to moderate travel may be used by the infant for foraging if the season is right for berries, fresh grass blades, flowers, or other foods that are easy for infants to obtain and process. This initial foraging may thereby produce a small immediate energetic tradeoff as well as provide opportunities for practice and learning that may be essential for eventual nutritional independence. By 8–10 months of age, Amboseli infants obtain almost 1000 kJ/day, more than half of their estimated nutritional intake, through independent feeding (S. Altmann, in preparation).

Carrying time declines much more rapidly with age than does suckling time (unpublished; also Nicolson 1982; Rhine et al. 1985; S. Altmann, in preparation), reflecting either differences in infant abilities or in maternal constraints, or an interaction between the two (see also Johnson 1986). We do know that direct behavioral conflict occurs during the transition to independent locomotion and involves mothers actively preventing their infants from riding when the infants try to do so (Altmann 1980).

In forcefully refusing to carry their infants, are mothers imposing behavior on the infants that is immediately more costly to the mother and perhaps also more costly for her future reproduction but that is developmentally essential for the infant? That is, at a certain age, does enforcing independent locomotion promote infant survival, even though it looks like rejection? Or are mothers providing less benefit to their infants and thereby reducing costs to their future reproduction? The answer will depend on the shape of the energetic intake and expenditure curves for mothers and for infants under various conditions, and on the effect of this energy balance on infant survival and on the mother's ability to invest in future offspring. Whether mothers and infants adjust their behavior in accord with short-term or long-term "payoffs" will also depend on their abilities, perceptual and otherwise, to detect and act on available information regarding the tradeoffs.

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